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The smallest stag beetles (Coleoptera, Lucanidae): hidden paleodiversity in mid-Cretaceous Kachin amber from northern Myanmar

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Abstract

The fossil record of stag beetles (Lucanidae), especially in Mesozoic amber, is sparse. Four additional fossil lucanids preserved in mid-Cretaceous Kachin amber from northern Myanmar are here reported. All of these species are included in the primitive subfamily Aesalinae, and have been identified as: *Protonicagus mandibularis* **sp. nov.** (tribe Nicagini); *Cretognathus minutissimus* **gen. et sp. nov.** (tribe Ceratognathini); Ceratognathini gen. et sp. indet. 1 (provisional assignment); and Ceratognathini gen. et sp. indet. 2 (provisional assignment). Except for *Protonicagus mandibularis* **sp. nov.**, the stag beetles appear to be connected to the continent of Gondwana, as with the Kachin amber paleofauna. More interestingly, these species have significantly smaller bodies than the extant species, with three of them measuring less than 3 mm, which makes them the smallest known species of Lucanidae. This finding is congruent with a trend toward miniaturization in several unrelated lineages of Kachin amber beetles, and it shows hidden paleodiversity of stag beetles during the Cretaceous.

Key Words

Aesalinae, Burmese amber, Cenomanian, Ceratognathini, fossil, Mesozoic, Nicagini, Scarabaeoidea

Introduction

With about 1800 species in 145 genera (Schoolmeesters 2023), stag beetles (Lucanidae) have a worldwide distribution throughout all main zoogeographical regions (Qi et al. 2022), but are particularly abundant and diversified in tropical regions, particularly in Southeast Asia (Mizunuma and Nagai 1994; Fujita 2010; Huang 2018; Yamamoto and Qodri 2022; Maquart et al. 2023). Many adult male lucanids have remarkably distinct mandibles as a sexual dimorphism, a feature that has attracted special attention; large males fight with other males using 'exaggerated' mandibles over females and food. Most species are saproxylic and found in forest habitats, with larvae feeding on deadwood at various stages of decomposition (Huang 2018), although some are known from sandy habitats along bodies of water and unvegetated dunes, such as *Nicagus* LeConte, 1861 (Tabana and Okuda 1992; Paulsen and Smith 2005; Tanahashi 2014).

Lucanids have long been considered one of the earliest-branching groups within the superfamily Scarabaeoidea, as evidenced by both morphological and molecular studies (Crowson 1967; Ratcliffe 2002; McKenna et al. 2015, 2019; Zhang et al. 2018; Cai et al. 2022). A recent molecular phylogenetic analysis of Lucanidae based on DNA information (Kim and Farrell 2015) implied that the current higher classification of lucanids needs substantial revision. Currently, Lucanidae are classified into eight subfamilies (Bouchard et al. 2011; Cai et al. 2017, 2022): four are extinct (Protolucaninae, Cerauchitinae, Paralucaninae, and Litholampriminae) and four are extant (Aesalinae, Syndesinae, Lampriminae, and Lucaninae). However, the validity of some of the fossil lucanid subfamilies has been questioned (Qi et al. 2022), which makes a re-evaluation of their systematic positions desirable. Notably, the overwhelming diversity is found in the subfamily Lucaninae, which accounts for more than 90% of all described species.

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By contrast, the extant subfamily Aesalinae contains 85 species placed in 12 extant and five extinct genera in three tribes: Aesalini MacLeay, Nicagini LeConte, and Ceratognathini Sharp (see Table 1 for the generic-level classification of Aesalinae; Paulsen and Mondaca 2006; Huang and Chen 2013, 2017; Paulsen 2013, 2018; Cai et al. 2017; Schoolmeesters 2023). Aesalinae is currently considered one of the early diverging lucanid lineages (Howden and Lawrence 1974; Scholtz 1990; Hosoya and Araya 2005; Kim and Farrell 2015). Unlike most lucanids, the aesalines are generally small beetles, with body lengths typically less than 10 mm (Holloway 2007; Paulsen 2013, 2018). They generally retain many plesiomorphic characters in Lucanidae, such as the entire eyes undivided by the ocular canthus, partially or not geniculate antennae, small mandibles, and some with strongly narrowed prosternal process resulting in subcontiguous procoxae (Kim and Farrell 2015). A few contradictory phylogenetic hypotheses for Aesalinae have been proposed. Hosoya and Araya (2005), Kim and Farrell (2015), and Kakizoe et al. (2023) have suggested the non-monophyly of Aesalinae, with the inclusion of Nicagini, whereas Paulsen (2013) established their monophyly in another molecular phylogenetic study and this view was supported by Reid (2019). Such conflicting results are mainly due to the elusive phylogenetic position of the tribe Nicagini among Lucanidae from molecular evidence (Hosoya and Araya 2005; Paulsen 2013; Kim and Farrell 2015) and morphology-based perspectives (e.g., Howden and Lawrence 1974; Tabana and Okuda 1992; Katovich and Kriska 2002; Holloway 2007).

Fossil Lucanidae are relatively rare, with about 30 species of fossil lucanids described from various fossil deposits worldwide, but mostly from Eurasia (Krell 2007; Jiang et al. 2022; Qi et al. 2022). Most are preserved as impression (compression) fossils with few observable characters, preventing accurate assessment of taxonomically or phylogenetically important traits in these fossils (Jiang et al. 2022). The earliest lucanid fossil taxon, *Juraesalus atavus* Nikolajev et al., 2011, is known from the Middle Jurassic Daohugou beds (ca. 165 Ma; Chen et al. 2004; Yang and Li 2008) of Inner Mongolia (Nikolajev et al., 2011), and is placed in either Aesalinae (Nikolajev et al., 2011) or the oldest crown group lucanid as Lucanidae *sensu stricto* (Kim and Farrell 2015). Four extinct lucanids have also been described as impression aesaline fossils: three species of the genus *Sinaesalus* Nikolajev et al., 2011 from the Lower Cretaceous (ca. 125 Ma; Swisher et al. 1999) Yixian Formation of Inner Mongolia (Nikolajev et al., 2011), and the monospecific genus *Cretaesalus* Nikolajev, 1993 from Upper Cretaceous (Turonian, 88.5–91 Ma; Gratshev and Zherikhin 2003) Kzyl-Zhar, Kazakhstan (Nikolajev 1993). Unlike impression fossils, amber fossils

Table 1. General overview of Aesalinae based on Schoolmeesters (2023), Li Y-D et al. (2023), and this study.

Genus-level classification	Described species (extinct species)/described subspecies	Distribution
Tribe Aesalini MacLeay, 1819	**46 (†5)/5**	Palaearctic, Oriental, Neotropical
1. *Aesalus* Fabricius, 1801	6/5	Palaearctic
-Subgenus *Aesalus* Fabricius, 1801	3/5	Palaearctic
-Subgenus *Huaesalus* Huang & Chen, 2017	3	Palaearctic
2. †*Cretaesalus* Nikolajev, 1993	†1	Kazakhstan (Upper Cretaceous)
3. *Echinoaesalus* Zelenka, 1993	7	Oriental including Taiwan
4. *Himaloaesalus* Huang & Chen, 2013	6	Palaearctic
5. †*Juraesalus* Nikolajev, Wang, Liu & Zhang, 2011	†1	China (Middle Jurassic)
6. *Lucanobium* Howden & Lawrence, 1974	2	Neotropical
7. †*Sinaesalus* Nikolajev, Wang, Liu & Zhang, 2011	†3	China (Lower Cretaceous)
8. *Strabaesalus* Paulsen, 2018	3	Oriental
9. *Trogellus* Paulsen, 2013	11	Neotropical
-Subgenus *Mayaesalus* Paulsen, 2013	3	Neotropical
-Subgenus *Trogellus* Paulsen, 2013	3	Neotropical
-Subgenus *Trogoides* Paulsen, 2013	5	Neotropical
10. *Zelenkaesalus* Krikken, 2008	6	Oriental
Tribe Ceratognathini Sharp, 1899	**36 (†2)**	Australian, Neotropical
1. *Ceratognathus* Westwood, 1838	14	Australian
2. †*Cretognathus* gen. nov.	†1	Myanmar (mid-Cretaceous Kachin amber)
3. *Hilophyllus* Paulsen & Mondaca, 2006	3	Neotropical
4. *Holloceratognathus* Nikolajev, 1998	3	Australian
5. *Mitophyllus* Parry, 1843	14	Australian
6. †*Oncelytris* Li & Cai, 2023 (in Li et al. 2023)	†1	Myanmar (mid-Cretaceous Kachin amber)
Tribe Nicagini LeConte, 1861	**5 (†2)**	Palaearctic, Nearctic
1. *Nicagus* LeConte, 1861	3	Palaearctic, Nearctic
2. †*Protonicagus* Cai, Yin, Liu & Huang, 2017	†2	Myanmar (mid-Cretaceous Kachin amber)
TOTAL: 18 (†6) genera, 5 subgenera	**87 (†9)/5**	

Although Schoolmeesters (2023) placed both †*Electraesalopsis* Bai, Zhang & Qiu, 2017 and †*Protonicagus* Cai, Yin, Liu & Huang, 2017 in the tribe Ceratognathini without evidence, I follow the systematic placements in the original descriptions (Bai et al. 2017; Cai et al. 2017) and treat them as 'subfamily *incertae sedis*' and Nicagini, respectively. The dagger marks indicate extinct taxa.

(fossilized tree resin) are generally more informative and sometimes allow more detailed analyses and comparisons with living counterparts (e.g., Cai et al. 2016; Yamamoto et al. 2017). Nevertheless, stag beetles are rarely found in amber, probably because their strength enabled them to escape from tree resin (Wu et al. 2022). Another factor would be generally large size of stag beetles with the preservation bias of amber to smaller insects (e.g., Song et al. 2022). Only nine lucanid species have been described as amber inclusions (Krell 2007; Jiang et al. 2022; Li Y-D et al. 2023): five from the mid-Cretaceous (near the Albian–Cenomanian boundary, 98.79 ± 0.62 Ma; Shi et al. 2012) Kachin amber of northern Myanmar (Cai et al. 2017; Qiu et al. 2017; Wu et al. 2022; Li Y-D et al. 2023); three from mid-Eocene (Lutetian, 44.1 ± 1.1 Ma; Wappler 2005) Baltic amber (Motschulsky 1857; Waga 1883; Zang 1905); and one from early Middle Miocene (15–20 Ma; Iturralde-Vinent and MacPhee 2019) Dominican amber (Woodruff 2009). The Kachin amber has drawn special attention in recent years and is an important source of lucanid fossils for assessing Mesozoic stag beetle diversity (Table 2).

Here, I report four lucanid specimens from mid-Cretaceous Kachin amber: a new species of *Protonicagus* (tribe Nicagini); a new genus with a new species (tribe Ceratognathini); Ceratognathini gen. et sp. indet. 1 (putative assignment); and Ceratognathini gen. et sp. indet. 2 (putative assignment). It is of note that three of these specimens are less than 3 mm in body length. This is unusual for stag beetles, which are often large (up to 120 mm including the mandibles; Fujita 2010). These fossils shed new light on the taxonomic and morphological paleodiversity of lucanid beetles during the Cretaceous.

Materials and methods

All the Kachin amber specimens used in this study were from amber deposits in Hukawng Valley (26°20'N, 96°36'E), Kachin State, northern Myanmar (Cruickshank and Ko 2003; Shi et al. 2012; Peretti 2020). A mid-Cretaceous age (Upper Albian to Lower Cenomanian) is adopted for amber material from this site (see further details in Balashov 2021). All of the fossil specimens, including the holotypes, are permanently housed in the Hokkaido University Museum (HUM), Hokkaido University, Sapporo, Japan (curator: M. Ôhara), under SEHU-0000121205 through 0000121208.

The amber pieces were trimmed with a fretsaw and ground with waterproof emery paper of different grit sizes. Then they were polished using plastic buffing cloths with an abrasive compound. Observations were made using either a Nikon SMZ 800 or 745T binocular stereomicroscope. To photograph these amber specimens, each amber piece was completely submerged in clove oil (Wako Pure Chemical Industries, Osaka, Japan) in a small Petri dish. As the refractive index 1.52–1.55 of clove oil is almost the same as that

Table 2. Checklist of Lucanidae in mid-Cretaceous Kachin amber, with their body lengths.

Taxon	Body length including mandibles	Body length excluding mandibles	Key references
Subfamily Aesalinae MacLeay, 1819			
Tribe Ceratognathini Sharp, 1899			
Genus †*Cretognathus* gen. nov.			This study
(type species: †*Cretognathus minutissimus* sp. nov.)			
1. †*Cretognathus minutissimus* gen. et sp. nov.	2.83 mm	2.80 mm	This study
Genus †*Oncelytris* Li & Cai, 2023			Li et al. (2023)
(type species: †*Oncelytris esquamatus* Li & Cai, 2023 (in Li et al. 2023))			
2. †*Oncelytris esquamatus* Li & Cai, 2023 (in Li et al. 2023)	N/A	about 4.0 mm	Li et al. (2023)
Ceratognathini, genus *incertae sedis*			
3. Ceratognathini gen. et sp. indet. 1	N/A	2.78 mm	This study
4. Ceratognathini gen. et sp. indet. 2	N/A	2.72 mm	This study
Tribe Nicagini LeConte, 1861			
Genus †*Protonicagus* Cai, Yin, Liu & Huang, 2017			Cai et al. (2017)
(type species: †*Protonicagus tani* Cai, Yin, Liu & Huang, 2017)			
5. †*Protonicagus tani* Cai, Yin, Liu & Huang, 2017	N/A	3.71 mm	Cai et al. (2017)
6. †*Protonicagus mandibularis* sp. nov.	3.78 mm	3.62 mm	This study
Subfamily Lucaninae Latreille, 1804			
Genus †*Anisoodontus* Wu, Tang & Peng, 2022 (in Wu et al. 2022)			Wu et al. (2022)
(type species: †*Anisoodontus qizhihaoi* Wu, Tang & Peng, 2022 (in Wu et al. 2022))			
7. †*Anisoodontus qizhihaoi* Wu, Tang & Peng, 2022 (in Wu et al. 2022)	17.36 mm	N/A	Wu et al. (2022)
8. †*Anisoodontus xiafangyuani* Wu, Tang & Peng, 2022 (in Wu et al. 2022)	11.80 mm	N/A	Wu et al. (2022)
Lucanidae, subfamily *incertae sedis*			
Genus †*Electraesalopsis* Bai, Zhang & Qiu, 2017 (in Qiu et al. 2017)			Qiu et al. (2017)
(type species: †*Electraesalopsis beuteli* Bai, Zhang & Qiu, 2017 (in Qiu et al. 2017))			
9. †*Electraesalopsis beuteli* Bai, Zhang & Qiu, 2017 (in Qiu et al. 2017)	5.6 mm	N/A	Qiu et al. (2017)

N/A, not available. The dagger marks indicate extinct taxa.

of amber, this reduced light reflection from the amber surface, increasing the quality of images of the lucanid inclusions. Most photographs were taken using either a Canon 80D or 90D digital camera equipped with a Canon MP-E 65 mm macro lens (f/2.8, 1–5×), and with a Canon MT-24EX twin flash as the light source. Several enlarged images had been obtained using a Canon EOS 6D digital camera attached to a Leica M205C stereomicroscope. The aquired images had been subsequently processed with Helicon Focus automontage software (ver. 7.7.5, 8.1.2, or 8.2.0) to expand the depth of field. All images were edited and assembled using Adobe Photoshop Elements 15. The morphological terminology generally follows Holloway (2007) and Cai et al. (2017). The subfamilial classification of Lucanidae follows Cai et al. (2022), although I acknowledge that the system adopted therein should be revised greatly in the future. The higher-resolution images are also available through the Zenodo repository (https://doi.org/10.5281/zenodo.8019509).

Systematic paleontology

Order Coleoptera Linnaeus, 1758
Superfamily Scarabaeoidea Latreille, 1802
Family Lucanidae Latreille, 1804
Subfamily Aesalinae MacLeay, 1819
Tribe Nicagini LeConte, 1861

Genus *Protonicagus* Cai, Yin, Liu & Huang, 2017

Type species. *Protonicagus tani* Cai, Yin, Liu & Huang, 2017.

Protonicagus mandibularis sp. nov.

https://zoobank.org/9689A395-8B60-46ED-BFC0-9E87158D2CA6
Figs 1A, B, 2–5

Material examined. ***Holotype*** (sex undertemined), a complete adult preserved in a somewhat cuboid yellowish amber with spherical upper surface, approximately 7.2 mm × 5.4 mm × 3.1 mm in size (Fig. 1A, B); specimen accession number SEHU-0000121205, housed in HUM. The holotype specimen is well preserved, but noticeable pigmentation inside the amber makes detailed observation and photography difficult. In addition, the ventral surface of the lucanid is covered with a thin whitish layer, which makes detailed observation even more difficult (Fig. 2B).

Differential diagnosis. *Protonicagus mandibularis* sp. nov. is most similar to *Protonicagus tani* Cai, Yin, Liu & Huang, 2017, also from Kachin amber, based on external morphological features in having a similar body size (3.62 *versus* 3.71 mm in *P. tani*), preocular margin (*sensu* Holloway 2007: fig. 3) of the eyes strongly enlarged and produced laterally, pronotal lateral margin rounded and strongly crenulate with a row of setae, similar structures and arrangements of outer teeth along the protibiae with strong spines in basal half, legs with short pretarsal claw, and each posterior margin of abdominal ventrites 2–4 armed with a row of villiform teeth. However, the new species is easily distinguished from the latter by its general habitus (narrowly elongate *versus* rounded and oval in *P. tani*), much larger non-acute apices of mandibles (acute in *P. tani*), dorsal surface densely covered with thin and long ground setae (rather than short scales as in *P. tani*; Cai et al. 2017: fig. 2B–D), much wider antennomeres 2–7,

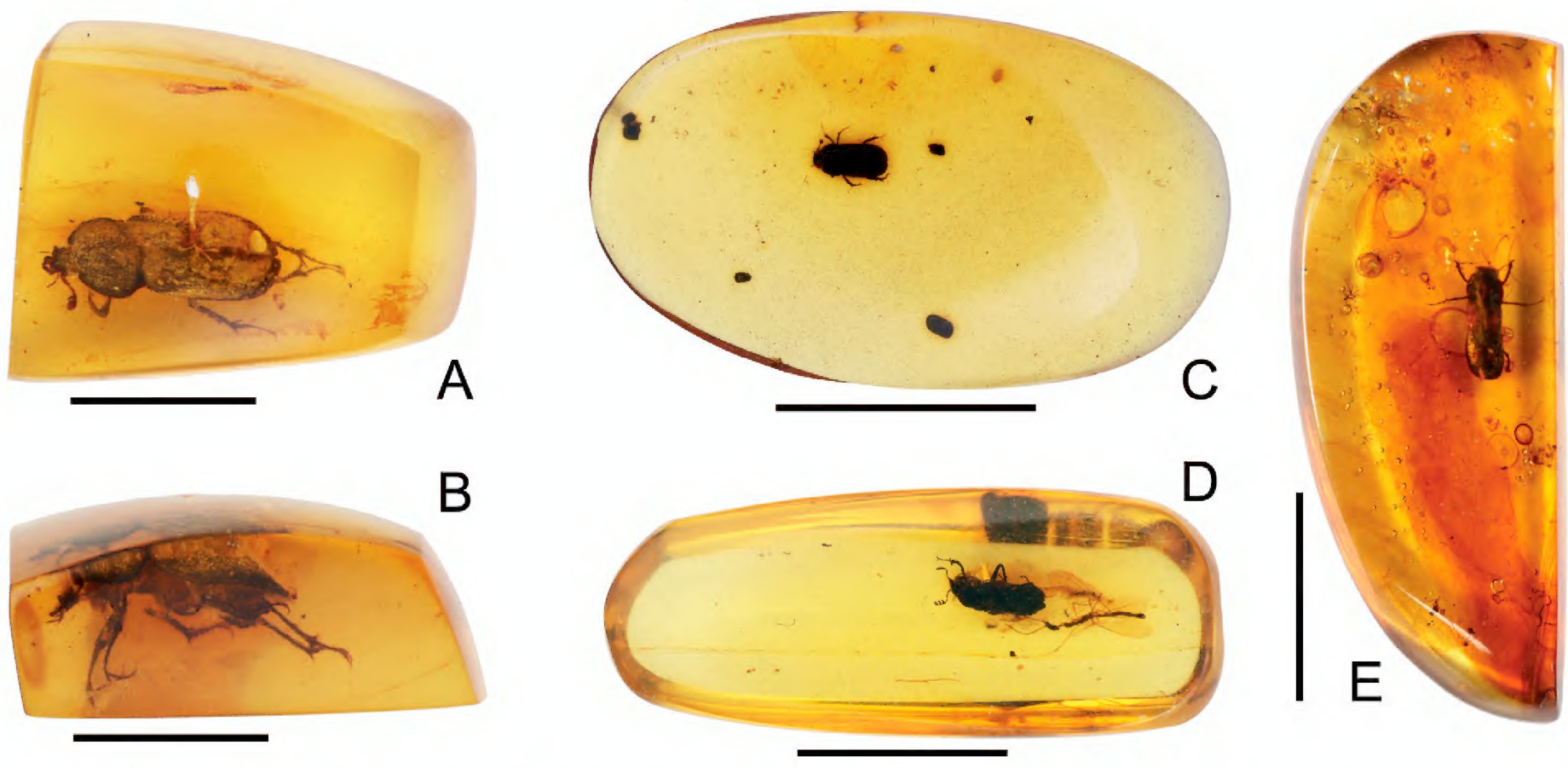

Figure 1. General view of amber pieces with lucanid inclusions. **A, B.** *Protonicagus mandibularis* sp. nov., holotype, SEHU-0000121205, showing dorsal (**A**) or lateral (**B**) views of the holotype; **C.** *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206; **D.** Ceratognathini gen. et sp. indet. 1, SEHU-0000121207; **E.** Ceratognathini gen. et sp. indet. 2, SEHU-0000121208. Scale bars: 3.0 mm (**A**, **B**); 1.0 cm (**C**); 5.0 mm (**D, E**).

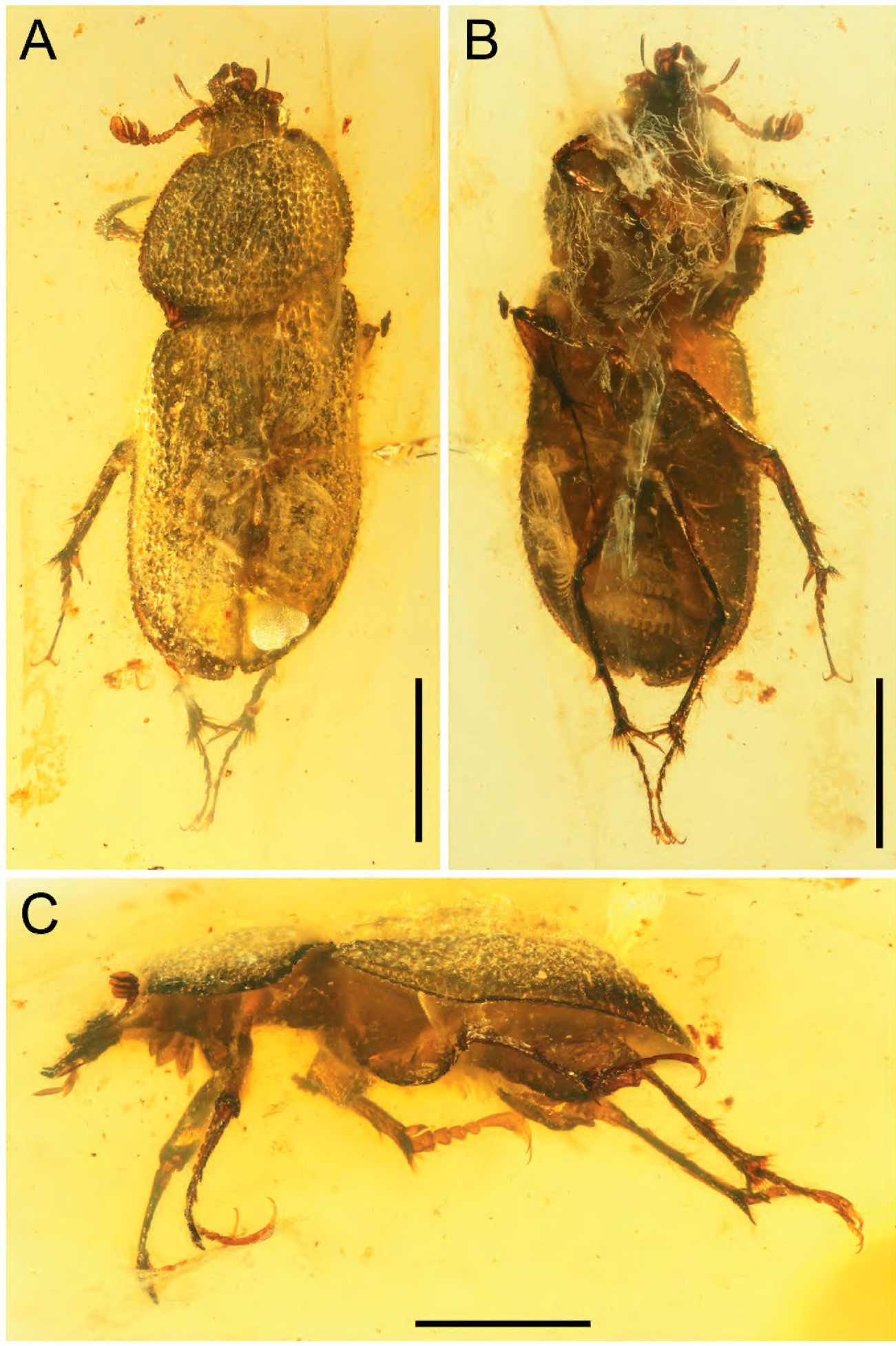

Figure 2. General habitus of *Protonicagus mandibularis* sp. nov., holotype, SEHU-0000121205. **A.** Dorsal view; **B.** Ventral view; **C.** Lateral view. Scale bars: 1.0 mm.

and obviously longer narrower metatarsi (see further details in Cai et al. 2017).

Diagnosis. Body small (ca. 3.6 mm), moderately elongate, subparallel sided (Fig. 2A, B). Dorsal surface covered with thin and long setae, lacking modified scales (Fig. 3). Antenna with spherical to transverse antennomeres 2–7 and three-segmented small club (Fig. 3A). Mandibles shorter than head, mostly visible dorsally, rather strongly curved and flattened, with rounded apices and nearly truncate apico-inner margins (Fig. 3A, B). Pronotum strongly and very densely punctate (Fig. 3C, D); lateral pronotal margins weakly crenulate, each with a row of setae (Fig. 3C, D, *rsp*). Outer protibial edge with one large apical tooth (*at*), one large and one smaller mid-dorsal teeth (*mdt1–2*), and less than ten generally subequal smaller tooth-like spines (Fig. 4A, B). Metatarsi long and slender, but shorter than metatibiae (Fig. 2).

Description. ***Body*** (Fig. 2) elongate oval, small, 3.62 mm long (measured from apex of clypeus to apex of elytra), 1.45 mm wide, moderately covex dorsoventrally. Color uniformly dark brown; antennae and mouthparts slightly paler. Dorsum (Figs 2A, 3) without modified scales, densely deeply punctate, setiferous punctures on pronotum and elytra large, each bearing suberect thin seta.

Head (Fig. 3A, B) small, rather strongly transverse, shorter than half pronotal length and narrower than half pronotal width, 0.44 mm long (measured from apex of clypeus to anterior margin of pronotum) and 0.57 mm

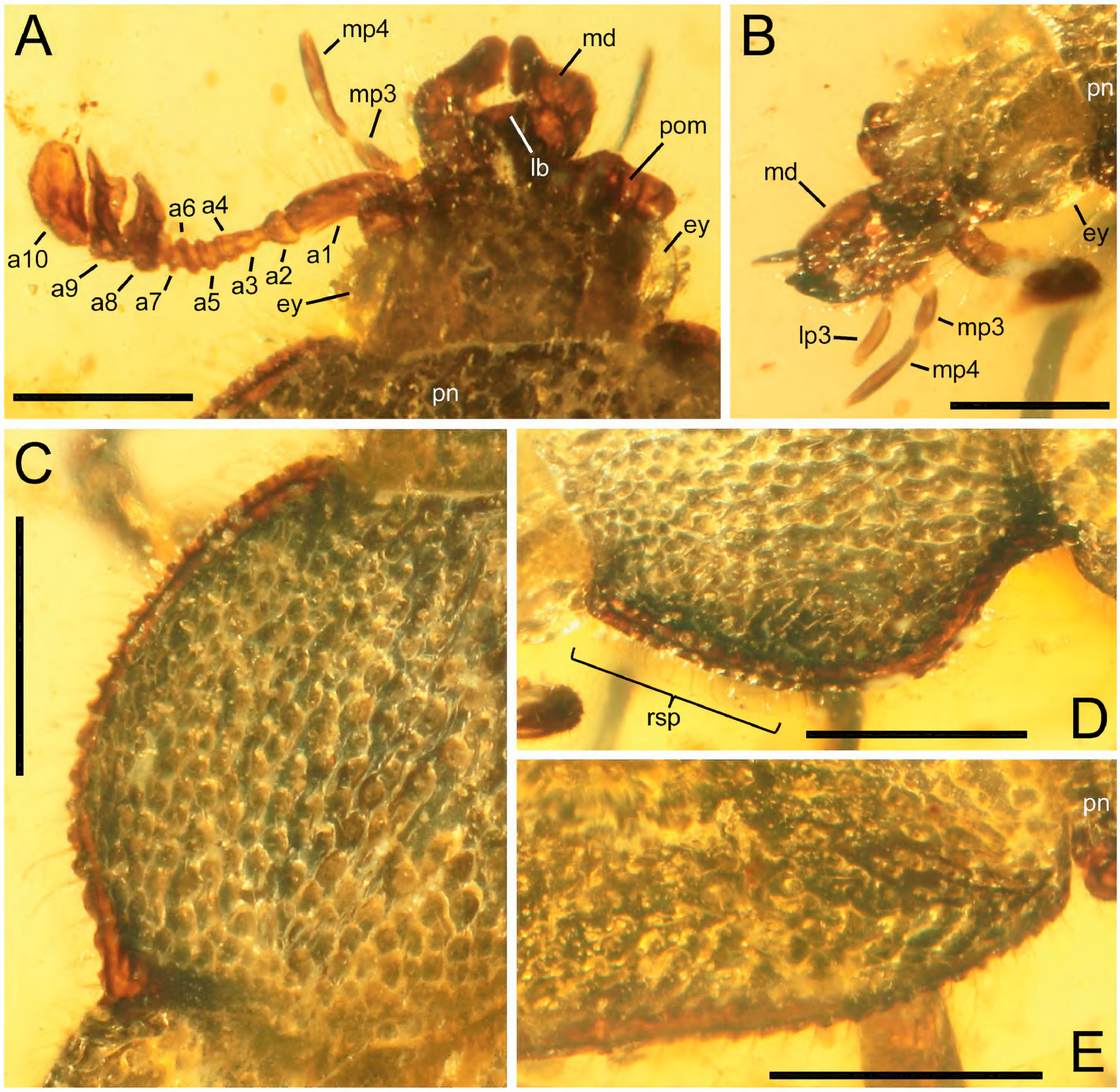

Figure 3. Details of *Protonicagus mandibularis* sp. nov., holotype, SEHU-0000121205. **A.** Head with left antenna, dorsal view; **B.** Head, dorsolateral view; **C.** Pronotum, left lateral half, dorsal view; **D.** Pronotum, dorsolateral view; **E.** Elytral base with shoulder, dorsolateral view. Abbreviations: a1–10, antennomeres 1–10; ey, compound eye; lb, labrum; lp3, labial palpomere 3; md, mandible; mp3–4, maxillary palpomeres 3–4; pn, pronotum; pom, preocular margin of head; rsp, row of setae along outer margin of pronotum. Scale bars: 0.3 mm (**A**, **B**); 0.5 mm (**C**, **D**, **E**).

wide across eyes; ventral side not well visible; vertex (Fig. 3A) densely punctate; preocular margins (Fig. 3A, *pom*) conspicuous, strongly enlarged, protruding anterolaterally. Compound eye (Fig. 3A, B, *ey*) relatively large, entire, not divided by ocular canthus. Antenna (Fig. 3A, *a1–10*) 10-segmented, non-geniculate, with three-segmented weakly lamellate club, 0.66 mm long (left antenna); antennomere 1 (scape) elongate, approximately 2.7 times longer than wide, sparsely bearing nine long and thin bristles, not covered with many setae; antennomere 2 (pedicel) very small, spherical, wider than long, with probably only a single bristle, attached to tip of scape; antennomeres 3–6 evenly weakly widened apicad; antennomere 3 small, as long as wide, narrower than preceding antennomere, weakly dilated apically; antennomere 4 moderately transverse, slightly wider than preceding antennomere; antennomere 5 rather strongly transverse, wider than preceding antennomere; antennomere 6 strongly transverse, moderately wider than preceding antennomere; antennomere 7 strongly transverse, slightly shorter than preceding antennomere; antennomeres 8–10 forming small and relatively loose club, strongly asymmetrical, each not coherent. Mandibles (Fig. 3A, B, *md*) mostly visible dorsally, slightly asymmetrical, small, shorter than head, bent strongly inward, dorsoventrally flattened and widened, not extending beyond maxillary

palps, with rounded, non-acute apex and nearly truncate apico-inner margin. Labrum (Fig. 3A, *lb*) small, transverse, with nearly truncate apex. Clypeus with produced anterior margin. Maxillary palpus (Fig. 3A, B, *mp3–4*) 4-segmented, moderately long, slender; palpomere 2 small; palpomere 3 spindle-shaped, widest in middle, about half length as terminal palpomere, with a long bristle near apex on outer margin; palpomere 4 very long, slender, fusiform, slightly bent inward near base, narrower than preceding palpomere. Labial palpus (Fig. 3B, *lp3*) probably three-segmented, long; palpomere 3 very long, slender, fusiform, slightly curved.

Pronotum (Figs 2A, 3C, D) transverse, widest in middle, 1.39 mm wide and 1.06 mm long (along midline), dorsally convex, with weak basolateral constriction; lateral margin (Fig. 3C, D) broadly rounded, modetately crenulate along whole margin, equipped with a row of ventrolaterally-directed long setae; surface simple and even; anterior corners slightly produced with obtuse angles, whereas those of posterior ones right-angled. Procoxal cavity externally closed behind. Prosternum short, seemingly strongly transverse; prosternal process between procoxae very narrow, resulting in subcontiguous procoxae (Fig. 5A, C, arrow).

Elytra (Figs 2A, C, 3E) complete, narrowly elongate, nearly subparallel-sided in anterior three-quarters, with left elytron 2.24 mm long (measured from pronotal posterior end to apex of elytron) and 0.70 mm wide; lateral margins serrulate, each with a row of setae; surface smooth without tubercles, but densely covered with deep dense setiferous punctures uniformly, seemingly not forming longitudinal rows (Fig. 3A). Mesocoxal cavities narrowly separated. Metaventrite (Fig. 5, *mtv*) transverse, much longer than mesoventrite; surface generally densely punctured, with short but prominent discrimen (median longitudinal sulcus; see Fig. 5, arrow).

Legs (Figs 2–5) relatively short. Protibia (Fig. 2A, B) robust, flattened, weakly curved, gradually widened apically, with one large apical spur; external margin armed with three strong teeth in apical half, i.e., one large, broadly pointed apical tooth (*at*), one large, broadly pointed mid-dorsal tooth 2 (*mdt2*), and one smaller but still prominent mid-dorsal tooth 1 (*mdt1*) (*sensu* Holloway 2007: fig. 1), with 9 short, acute, and generally subequal smaller tooth-like spines (8 subcontiguous ones between base and *mdt1*, 1 between *mdt1* and *mdt2*, and 0 between *mdt2* and *at*, see arrows on Fig. 4A, B, E for the latter condition). Procoxa widely transverse. Mesotibia with three small mid-dorsal spines at middle (Fig. 4H, *mds*), with paired apical spurs (Fig. 4C, G, H, *as*). Metacoxae (Fig. 5, *mtc*) transverse, subcontiguous. Metatibia (Fig. 4B) slender, only slightly longer than metatarsus, with three small mid-dorsal spines located at slightly beyond middle apically (Fig. 4D, F, *mds*) and paired prominent apical spurs (Fig. 4D, F, *as*). All tarsi 5-segmented, each slender and rather long; tarsomere 1 longer than tarsomere 2, tarsomeres 2–4 subequal in length, tarsomere 5 longest, as long as tarsomeres 2–4 combined (Fig. 4A, C–H). Pretarsal claw (Fig. 4A, C–H, *cl*) short, simple, moderately curved, shorter than tarsomeres 3 and 4 combined. Arolium (Fig. 4C, D, G, H) developed, with short rod (Fig. 4D, *ra*), bearing 2 bristles on its apex (Fig. 4D, *sa*).

Abdomen (Figs 2B, 5B) with 5 visible ventrites (*v1–5*); central part rather swelled above; each ventrite strongly transverse; ventrites 2–4, at least, each armed with a row of large villiform teeth along posterior margin; ventrite 5 with posterior margin broadly arcuate.

Genitalia not visible.

Etymology. The specific name "*mandibularis*" (Latin *mandibulum* + *-aris*) refers to its unusual shape of the mandibles.

Locality and horizon. Hukawng Valley (26°20'N, 96°36'E), Kachin State, northern Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Systematic placement and comparison. *Protonicagus mandibularis* sp. nov. can be assigned to the scarabaeoid family Lucanidae based on the narrowly elongate body shape, 10-segmented antennae with three-segmented, non-coherent, lamellate apical club, anteriorly projecting and rather developed mandibles, 5–5–5 tarsal formula, protibial structures with characteristic outer teeth, developed bisetose arolium between the pretarsal claws, and five visible abdominal ventrites (e.g., Ratcliffe 2002; Holloway 2007; Cai et al. 2017; Reid 2019). Furthermore, the fossil taxon is assigned to the ancestral extant subfamily Aesalinae based on its non-geniculate antennae, complete eyes (not divided by ocular canthus), small mandibles, non-striate elytra, and strongly narrowed prosternal process with subcontiguous procoxae. It is easily separated from the New Zealand endemic Lampriminae, *Dendroblax earlii* White with a *Nicagus*-like body and short mandibles in both sexes, by the considerably different locations and shapes of the protibial outer teeth, distinctly smaller body size, glabrous metaventrite, and much longer linear antennomere 1 (cf. Fujita 2010; Bartolozzi et al. 2017). Within Aesalinae, the new species is similar externally to the extinct genus *Protonicagus*, also from Kachin amber (tribe Nicagini), including the similar body size, notably enlarged lateral margins of preocular margin of the eyes, rounded lateral margin of the pronotum with strong crenulation bearing a row of setae, similar structures of the protibiae, and abdominal ventrites 2–4 each armed with a row of villiform teeth (Cai et al. 2017). However, I found several distinct features that do not match *P. tani*, the sole member of *Protonicagus*: 1) much narrower, elongate body; 2) clearly larger non-acute mandibles; 3) absence of dense, inclined, linear scales on the pronotum and elytra, but covered with thin, long setae; 4) much wider antennomeres 2–7; and 5) obviously longer and narrower metatarsi with longer tarsomeres 1 (cf. Cai et al. 2017). From the sole extant genus *Nicagus* in Nicagini, *P. mandibularis* sp. nov. is ruled out mainly by the characters mentioned in Cai et al. (2017) and described above. Therefore, I prefer to tentatively include it in *Protonicagus* because of the general morphological similarity.

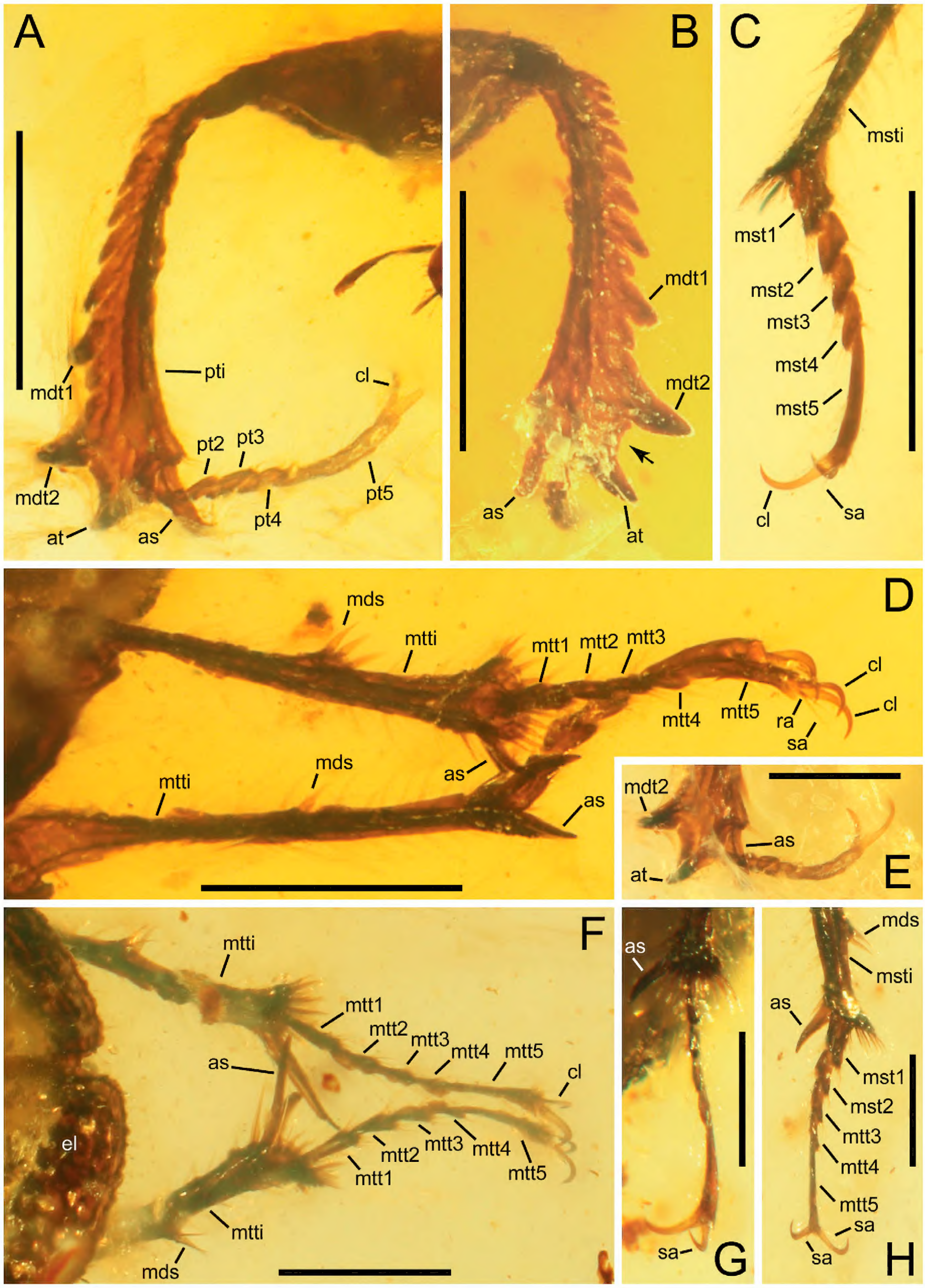

Figure 4. Details of *Protonicagus mandibularis* sp. nov., holotype, SEHU-0000121205. **A.** Right protibia and protarsus, frontal view; **B.** Left protibia with arrow showing absence of small teeth between large spines along outer edge of protibia, frontal view; **C.** Left mesotibia and mesotarsus, dorsolateral view; **D.** Metatibiae and metatarsi, lateral view; **E.** Apex of right protibia, frontal view; **F.** Metatibiae and metatarsi, dorsal view; **G.** Left mesotarsus, ventrolateral view; **H.** Left mesotarsus, ventral view. Abbreviations: as, apical spur; at, apical tooth of protibia; cl, claw; el, elytron; mds, mid-dorsal spines of meso- and metatibia; mdt1–2, mid-dorsal teeth 1–2 of protibia; mst1–5, mesotarsomeres 1–5; msti, mesotibia; mtt1–5, metatarsomeres 1–5; mtti, metatibia; pt2–5, protarsomeres 2–5; pti, protibia; ra, rod of arolium; sa, setae on rod of arolium. Scale bars: 0.5 mm (**A–D**, **F**); 0.3 mm (**E**, **G**, **H**).

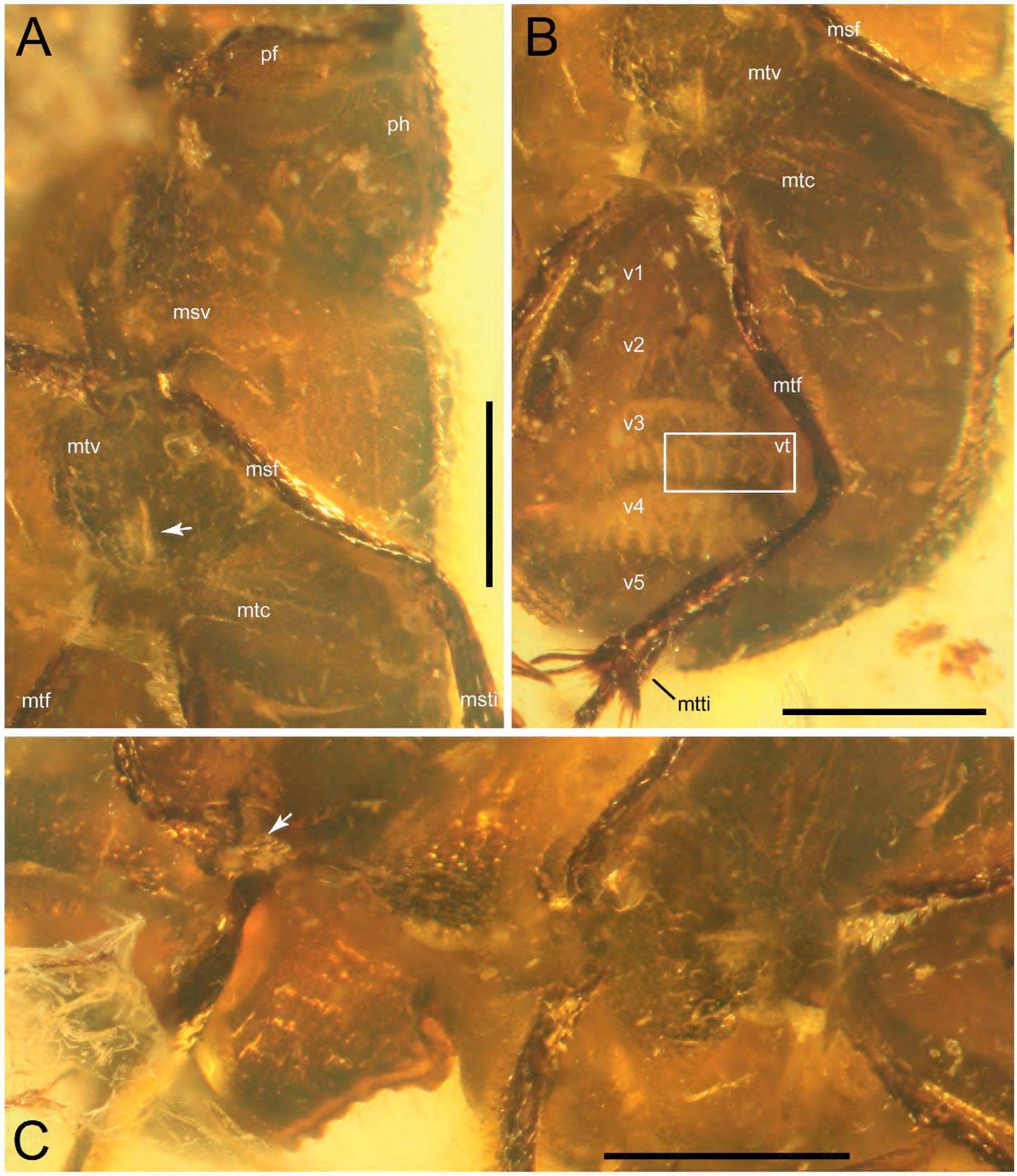

Figure 5. Details of *Protonicagus mandibularis* sp. nov., holotype, SEHU-0000121205. **A.** Meso- and metathorax with arrow showing discrimen (median longitudinal sulcus) on metaventrite, ventral view; **B.** Metathorax and abdomen, ventral view; **C.** Pro-, meso-, and metathorax with arrow showing subcontiguous procoxae, ventral view. Abbreviations: msf, mesofemur; msti, mesotibia; msv, mesoventrite; mtc, metacoxal cavity; mtf, metafemur; mtti, metatibia; mtv, metaventrite; pf, profemur; ph, pronotal hypomeron; v1–5, ventrites 1–5; vt, row of villiform teeth on margins of ventrites. Scale bars: 0.5 mm (**A**, **B**); 0.3 mm (**C**).

Given the distinct morphological differences in lucanid species due to sexual dimorphism, it is difficult to determine whether such differences are interspecific characters within the genus or just individual variation between the different sexes of the same species. I have considered these morphological differences to be interspecific rather than sexual dimorphism and it is hereby described as a new species. This conclusion is supported by the marked morphological differences. For example, the extant sole nicagin genus *Nicagus* has generally similar body shapes in both sexes (Paulsen and Smith 2005), unlike the great differences seen in the fossil presented here and *P. tani*. Similarly, the body surface of *P. mandibularis* sp. nov. lacks short distinct scales, which should be considered an interspecific difference rather than a sexual difference.

Key to species of *Protonicagus*

1 Body oval, rounded; pronotum and elytra covered with short and flattened scales; antennomere 2 elongate; mandibles inconspicuous, largely not well exposed, with acute apex; metatarsi short, robust..... *P. tani* Cai, Yin, Liu & Huang, 2017

– Body elongate oval; pronotum and elytra covered with long and thin setae; antennomere 2 transverse; mandibles rather conspicuous, largely exposed, with non-acute apex; metatarsi long and slender, only slightly shorter than metatibiae ..... *P. mandibularis* sp. nov.

Tribe Ceratognathini Sharp, 1899

Genus *Cretognathus* gen. nov.

https://zoobank.org/0EF18D3E-DC80-4E51-A14E-982C18DA3E51

Figs 1C, 6–10

Type species. *Cretognathus minutissimus* sp. nov., here designated.

Differential diagnosis. *Cretognathus* gen. nov. is easily separated from all known extant ceratognathin genera from the Australian Region, except the extant *Holloceratognathus passaliformis* (Holloway), by the complete lack of modified scales on the dorsal surface (Figs 6A, 8). It can be distinguished from *H. passaliformis* by the absence of several derived features, such as widely explanate pronotal and elytral margins and distinctly paddle-shaped tibiae (Holloway 2007). *Cretognathus* gen. nov. is somewhat similar to the recently described ceratognathin genus *Oncelytris* Li & Cai, 2023 (in Li Y-D et al. 2023) from Kachin amber in the absence of dosal scales (Li Y-D et al. 2023). However, the distinctly tuberculate elytra of *Oncelytris* are unusual in the family (Li Y-D et al. 2023), and *Cretognathus* gen. nov. apparently lacks such distinct tubercles on the dorsum of elytra.

Diagnosis. Body very small, moderately elongate oval, rather flattened; body length well below 3.0 mm. Dorsal surface lacks neither modified scales nor setae (Figs 6A, 8). Head with broadly rounded anterior margin (Fig. 7A); vertex simple, without a pair of protuberances (Fig. 7A). Antenna non-geniculate, with three-segmented, rather strong club (Fig. 7A, B, D). Mandibles small, inconspicuous, bearly visible dorsally, with sharply pointed apices (Fig. 7A–C). Pronotum densely strongly punctate (Fig. 8A); lateral pronotal margins smooth, with very narrow gutter along whole margins (Fig. 8A, D). Prosternum biconcaved; prosternal process strongly narrowed and laminate between procoxae, resulting in subcontiguous procoxae (Fig. 10A). Elytra smooth without distinct tubercles and evident rows of punctures (Fig. 8B, C, E); lateral margin with narrow epipleural gutter. Outer protibial margin with one large, curved, and slender apical tooth (*at*), one large, curved, and slender mid-dorsal tooth 2 (*mdt2*), one smaller mid-dorsal tooth 1 (*mdt1*), and about 16 subequal smaller teeth (Fig. 9A, B).

Included species. Only *Cretognathus minutissimus* sp. nov.

Etymology. The generic name is composed of the prefix *Creto-* from "Cretaceus" referring to the "Cretaceous age" of the extinct genus and the type genus *Ceratognathus* Westwood, 1838 of Ceratognathini. It is masculine in gender.

Systematic placement and comparison. *Cretognathus* gen. nov. can be unambiguously assigned to the scarabaeoid family Lucanidae based on the moderately elongate and rather dorsoventrally flattened body shape, 10-segmented antennae with a relatively long antennomere 1 and three-segmented, non-coherent and lamellate apical club, 5–5–5 tarsal formula, protibial structures with characteristic outer teeth, strongly developed bisetose arolium between the pretarsal claws, and five visible abdominal ventrites (e.g., Ratcliffe 2002; Holloway 2007; Cai et al. 2017; Reid 2019). Furthermore, the new genus can be safely attributed to the plesiomorphic extant subfamily Aesalinae based on its non-geniculate antennae with a three-segmented club, complete eyes (not divided by ocular canthus), small mandibles, non-striate elytra, and strongly narrowed prosternal process with subcontiguous procoxae (e.g., Holloway 2007; Reid 2019). Among the three tribes of Aesalinae, *Cretognathus* gen. nov. is separated from Nicagini by a combination of the following character states (Paulsen 2005): complete absence of evident ground scales (setae) on the dorsum, much longer setae of the arolium, and particularly the features of the outer protibial edge (i.e., apical tooth (*at*) much narrower and pointed, mid-dorsal tooth (*mdt2*) much longer and slenderer, located anteriorly, mid-dorsal tooth (*mdt1*) narrower with acute apex, and the presence of subequal smaller teeth between apical tooth and mid-dorsal tooth 2) (see Fig. 15 for the comparison). Furthermore, the new genus is easily distinguished from Aesalini in having a strongly narrowed prosternal process and subcontiguous procoxae (see Huang et al. 2009). Overall, the general morphology of *Cretognathus* gen. nov. matches the remaining tribe Ceratognathini, particularly based on the structures of the protibial edges. In fact, the new genus has the typical pattern of protibial spines. Consequently, it is best placed within Ceratognathini.

Ceratognathini is a small tribe with only four extant genera (Table 1): *Ceratognathus* Westwood, 1838; *Hilophyllus* Paulsen & Mondaca, 2006; *Holloceratognathus* Nikolajev, 1998; and *Mitophyllus* Parry, 1843 (Holloway 1998, 2007; Paulsen and Mondaca 2006; Paulsen 2013). In addition, the extinct genus *Oncelytris* from Kachin amber was very recently described (Li Y-D et al. 2023). Although these extant genera share externally similar habitus and body parts, they are mainly identified by the different structures and arrangements of the smaller protibial outer teeth-like spines (Holloway 1998, 2007; Paulsen and Mondaca 2006). Unlike *Holloceratognathus* which has numerous variably sized small spines, the new

Figure 6. General habitus of *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206. **A.** Dorsal view; **B.** Ventral view. Scale bars: 1.0 mm.

genus has numerous small, equal spines elsewhere along the outer edges of the protibiae (cf. Holloway 1998, 2007; Paulsen and Mondaca 2006). It is somewhat difficult to compare the new taxon with the three other extant ceratognathinin genera in further detail based on the structures and arrangements of the protibial teeth, but *Cretognathus* gen. nov. has relatively large teeth-like spines between the base and mid-dorsal tooth 2 (i.e., mid-dorsal tooth 1, *mdt1*, in this paper) along with the similar condition in *Ceratognathus*. Nevertheless, the new genus cannot be placed in *Ceratognathus* due to the lack of a pair of protuberances or tubercles (raised shiny patches) on the dorsal side of the head (Holloway 2007). More importantly, no ground setation or modified scales are found on the dorsal surface of *Cretognathus* gen. nov. (Fig. 8). This condition has never been observed in any recent ceratognathinin (Fig. 15), including the *Ceratognathus* species, with the only exception *H. passaliformis* (see also Bartolozzi et al. 2017). Interestingly, however, the other Kachin amber ceratognathinin *Oncelytris* also lacks such modified scales on the elytra (Li Y-D et al. 2023).

From all of the lucanid fossils so far described from Kachin amber, *Cretognathus* gen. nov. can be readily separated from *Anisoodontus* Wu, Tang & Peng, 2022 (in Wu et al. 2022) (Lucaninae) in having a much smaller body (11.80–17.36 mm, including mandibles, in *Anisoodontus*), non-geniculate antennae, and short, inconspicuous mandibles (cf. Wu et al. 2022); from *Protonicagus* (Aesalinae: Nicagini) by non-crenulate pronotal lateral margins without a row of setae, larger head with non-enlarged preocular margin of the eyes, absence of any dorsal scales or ground setae, and presence of small subcontiguous teeth-like spines between the apical tooth and mid-dorsal tooth 2 (cf. Cai et al. 2017; this study); from *Electraesalopsis* Bai, Zhang & Qiu, 2017 (in Qiu et al. 2017) (subfamily *incertae sedis*) by the presence of much shorter, unmodified mandibles, much strongly developed antennal club, broadly rounded clypeal margin, distinctly shorter metatarsi, smaller body (5.6 mm, including mandibles, in *Electraesalopsis*), and structures of the protibiae with their strongly developed apical teeth (cf. Qiu et al. 2017); from *Oncelytris* by the lack of a pair of not well-separated protuberances and tuberculate elytra. Consequently, the new genus can easily be distinguished from any fossil genera described from Kachin amber. Furthermore, *Cretognathus* gen. nov. is separated from the two undetermined provisional ceratognathins reported below, mainly by the shape of the protibiae and antennae (the latter can be applied only for Ceratognathini gen. et sp. indet. 1).

Cretognathus minutissimus sp. nov.

https://zoobank.org/A12A7EF3-8BE0-4BB2-9F23-130C6B7F9313

Figs 1C, 6–10

Material examined. ***Holotype*** (sex undertemined), a complete adult preserved in a large, very flat, oval yellowish amber, approximately 24.5 mm × 14.4 mm × 1.9 mm in size (Fig. 1C); specimen accession number

SEHU-0000121206, housed in HUM. The holotype specimen is well preserved, but pigmentation inside the amber makes detailed observation and photography difficult, particularly of the ventral side. Furthermore, the ventral surface of the holotype is very dark; therefore, it is difficult to observe and photograph.

Diagnosis. As for the genus (*vide supra*).

Description. ***Body*** (Fig. 6) very small, moderately elongate oval, 2.80 mm long (measured from apex of clypeus to apex of elytra), 1.28 mm wide, rather flattened dorsoventrally. Color uniformly dark brown; antennae and mouthparts slightly paler. Dorsum (Figs 6A, 8) glabrous, lacking modified scales; pronotum and elytra with dense, large punctures.

Head (Fig. 7A–C) relatively small, transverse, shorter than half pronotal length but wider than half pronotal width, 0.44 mm long (measured from apex of clypeus to anterior margin of pronotum) and 0.76 mm wide across eyes (Fig. 7A, C); ventral side not well visible; vertex (Fig. 7A) even, smooth, only weakly punctate, without a pair of tubercles; preocular margins (Fig. 7A, C, *pom*) small, arcuate, not enlarged anterolaterally. Compound eye (Fig. 7, *ey*) relatively large, entire, not divided by ocular canthus. Antenna (Fig. 7A, B, D, *a1–10*) 10-segmented, non-geniculate, with three-segmented relatively strong club, 0.55 mm long (right antenna); antennomere 1 (scape) long, slender, rather strongly curved, approximately 4.7 times longer than wide, sparsely bearing three very long and thin bristles and much shorter seta, without ground setae; antennomere 2 (pedicel) small, conical, somewhat transverse, attached to tip of scape; antennomere 3 elongate, about 1.9 times longer than wide; antennomeres 4–6 short, each wider than length, successively moderately widened; antennomere 7 shorter than preceding antennomere, but distinctly transverse; antennomeres 8–10 forming relatively large club, strongly asymmetrical, each not coherent. Mandibles (Fig. 7A–C, *md*) mostly not visible dorsally, very small, inconspicuous, much shorter than head, moderately curved, dorsoventrally flattened, with acute, sharply pointed apex. Clypeus with broadly rounded anterior margin. Maxillary palpus (Fig. 7A–C, *mp3–4*) 4-segmented, moderately long, slender; palpomere 2 small; palpomere 3 elongate, about half length as terminal palpomere, weakly curved; palpomere 4 very long, slender, gently arcuate, slightly wider than preceding palpomere. Labial palpus (Fig. 7B, *lp3*) probably three-segmented, rather short; palpomere 3 long, fusiform.

Pronotum (Figs 6A, 8A–D) transverse, widest in middle, 1.21 mm wide and 0.87 mm long (along midline), without basolateral constriction; lateral margin gently arcuate, smooth, with very narrow gutter along whole margins (Fig. 8D, *pg*); surface simple and even, but densely strongly punctate; anterior corners slightly produced with acute angles, whereas those of posterior ones right-angled. Procoxal cavity externally closed behind. Prosternum short, biconcaved, seemingly strongly transverse; prosternal process between procoxae very narrow, laminate, resulting in subcontiguous procoxae (Fig. 10A, arrow). Scuteller shield (Fig. 8A–C, *sc*) small, semicircular; surface even, entirely covered with rather dense, deep punctation.

Elytra (Figs 6A, 8B, E, 9C, D) complete, narrowly elongate, nearly subparallel-sided in anterior four-fifths, with left elytron 1.71 mm long (measured from pronotal posterior end to apex of elytron) and 0.66 mm wide; lateral margins narrowly explanate, each with inconspicuous epipleural gutter (see Yamamoto 2021) (Fig. 8B, E 9C, D, *epg*); surface smooth without tubercles, but densely covered with deep dense punctures uniformly, seemingly not forming evident longitudinal rows (Fig. 8B). Mesocoxal cavities narrowly separated (see Fig. 10B). Metaventrite (Fig. 10B–D, *mtv*) transverse, much longer than mesoventrite; surface generally somewhat densely punctured, with deep and prominent discrimen (median longitudinal sulcus; see Fig. 10D, arrow).

Legs (Figs 6, 9, 10) short, rather thick, robust (except very slender protarsi). Protibia (Figs 6, 9A, B) robust, flattened, weakly curved, gradually widened apically, with one large apical spur; external edge armed with three strong teeth in apical half, i.e., one large, curved, and slender apical tooth (*at*), one large, curved, and slender mid-dorsal tooth 2 (*mdt2*), and one smaller, inconspicuous mid-dorsal tooth 1 (*mdt1*) (*sensu* Holloway 2007: fig. 1), with 16 short, acute, and subequal-sized tooth-like spines (8 subcontiguous ones before *mdt1*, 4 subcontiguous ones between *mdt1* and *mdt2*, and 4 subcontiguous ones between *mdt2* and *at*, see arrows on Fig. 9A, B for the latter condition). Procoxa widely transverse. Mesotibia with a few small mid-dorsal spines at apical two-fifths (Fig. 9C, *mds*), with paired prominent apical spurs (Fig. 9C, E, F, *as*). Metacoxae (Fig. 10C, D, *mtc*) transverse, subcontiguous. Metatibia (Fig. 9D) thick and robust, only slightly longer than metatarsus, with a few small mid-dorsal spines located at slightly beyond middle apically (Fig. 9D) and paired prominent apical spurs (Fig. 9D, G, H, *as*). All tarsi 5-segmented, each extremely slender and long (protarsi) or thick and rather short (meso- and metatarsi); tarsomere 1 longer than tarsomere 2, tarsomeres 2–4 subequal in length, tarsomere 5 longest, as long as (protarsi) or slightly shorter (meso- and metatarsi) than tarsomeres 2–4 combined (Fig. 9). Pretarsal claw (Fig. 9, *cl*) relatively short, simple, moderately curved, moderately (protarsi) or slightly (meso- and metatarsi) shorter than tarsomeres 3 and 4 combined. Arolium (Fig. 9) well-developed, with elongate rod (Fig. 9, *ra*), bearing 2 long bristles on its apex (Fig. 9, *sa*).

Abdomen (Figs 6B, 10C, D) with 5 visible ventrites (*v1–5*); central part rather swelled above; each ventrite strongly transverse; ventrites 2–4, at least, each armed with a row of large villiform teeth along posterior margin; ventrite 5 with apical margin only feebly emarginate (similar condition of the male of *Mitophyllus* figured in Holloway 1998: fig. 19).

Genitalia not visible.

Etymology. The specific name "*minutissimus*" is a Latin adjective meaning 'extremely small', in reference to its very small body size for the Lucanidae family.

Locality and horizon. Hukawng Valley (26°20'N, 96°36'E), Kachin State, northern Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

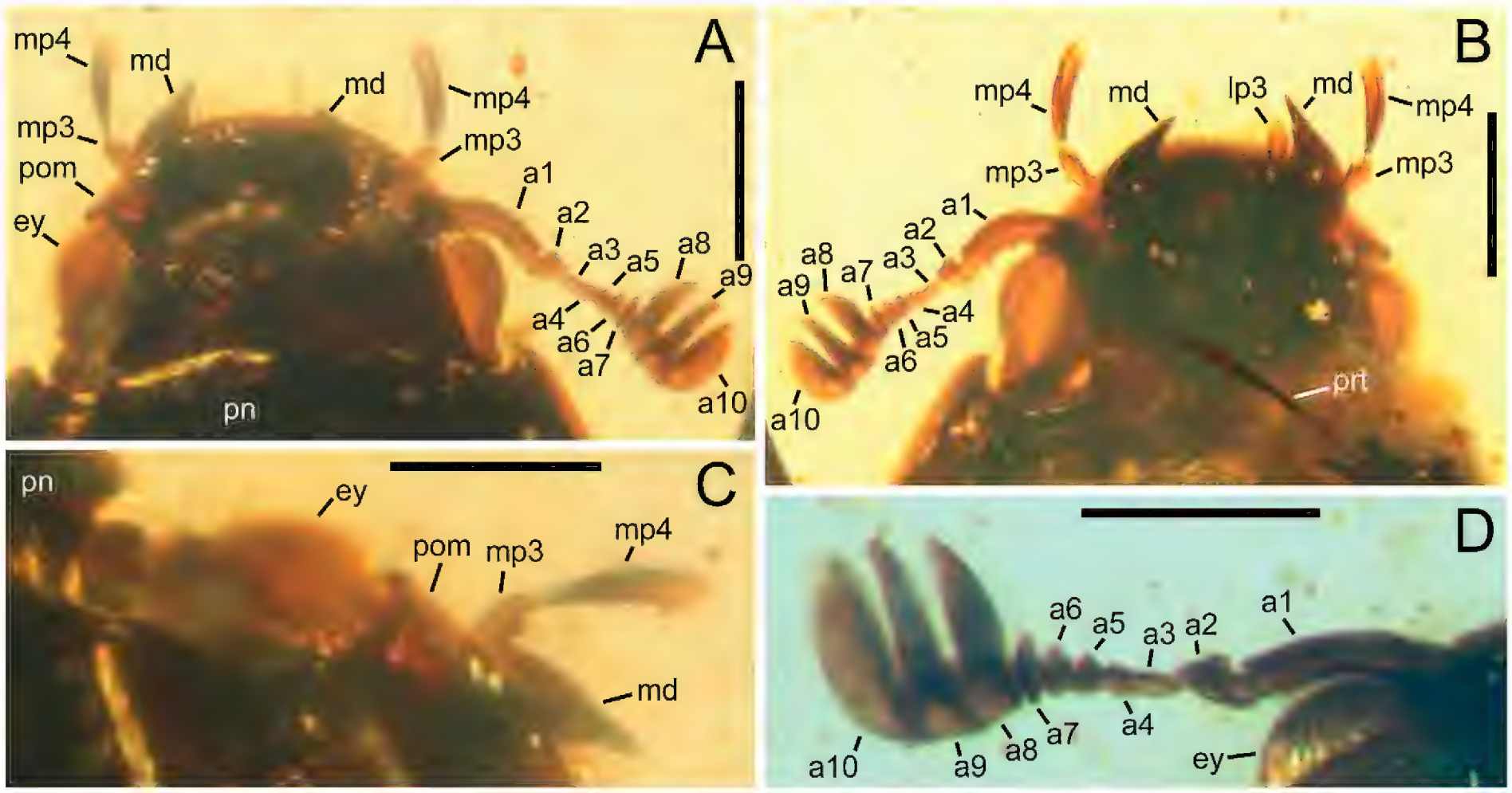

Figure 7. Details of *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206. **A.** Head with right antenna, dorsal view; **B.** Head with right antenna, ventral view; **C.** Enlargement of **A**; **D.** Right antenna, ventral view. Abbreviations: a1–10, antennomeres 1–10; ey, compound eye; lp3, labial palpomere 3; md, mandible; mp3–4, maxillary palpomeres 3–4; pn, pronotum; pom, preocular margin of head; prt, protarsus. Scale bars: 0.3 mm (**A**, **B**); 0.2 mm (**C**, **D**).

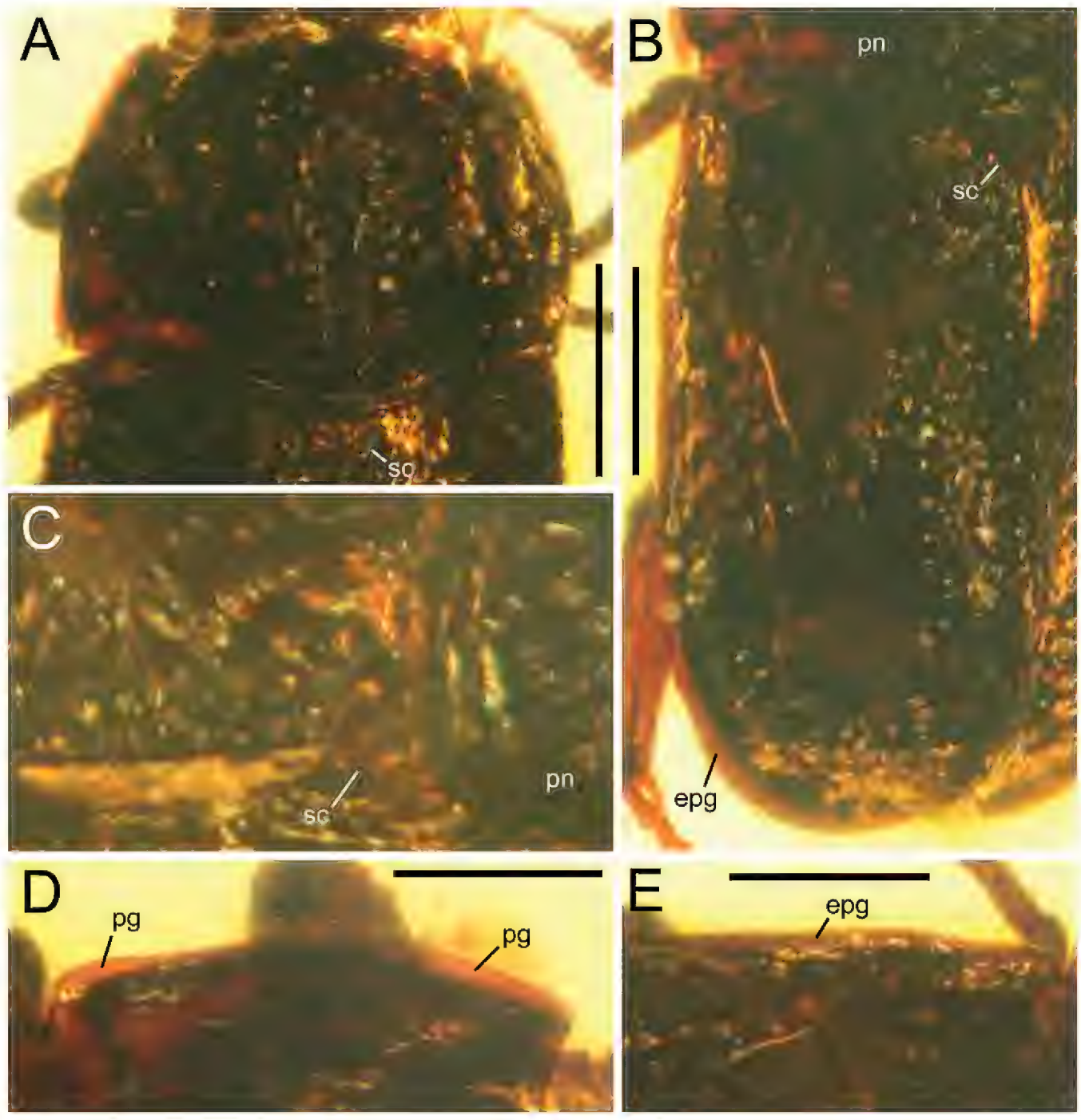

Figure 8. Details of *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206. **A.** Pronotum and elytral base, dorsal view; **B.** Left elytron, dorsolateral view; **C.** Punctation on elytra, pronotum, and scutellar shield; **D.** Left lateral margin of pronotum, dorsal view; **E.** Left elytral margin with elytral shoulder, dorsal view. Abbreviations: epg, epipleural gutter along outer margin of elytron; pg, gutter along outer margin of pronotum; pn, pronotum; sc, scutellar shield. Scale bars: 0.5 mm (**A**, **B**, **E**); 0.3 mm (**D**).

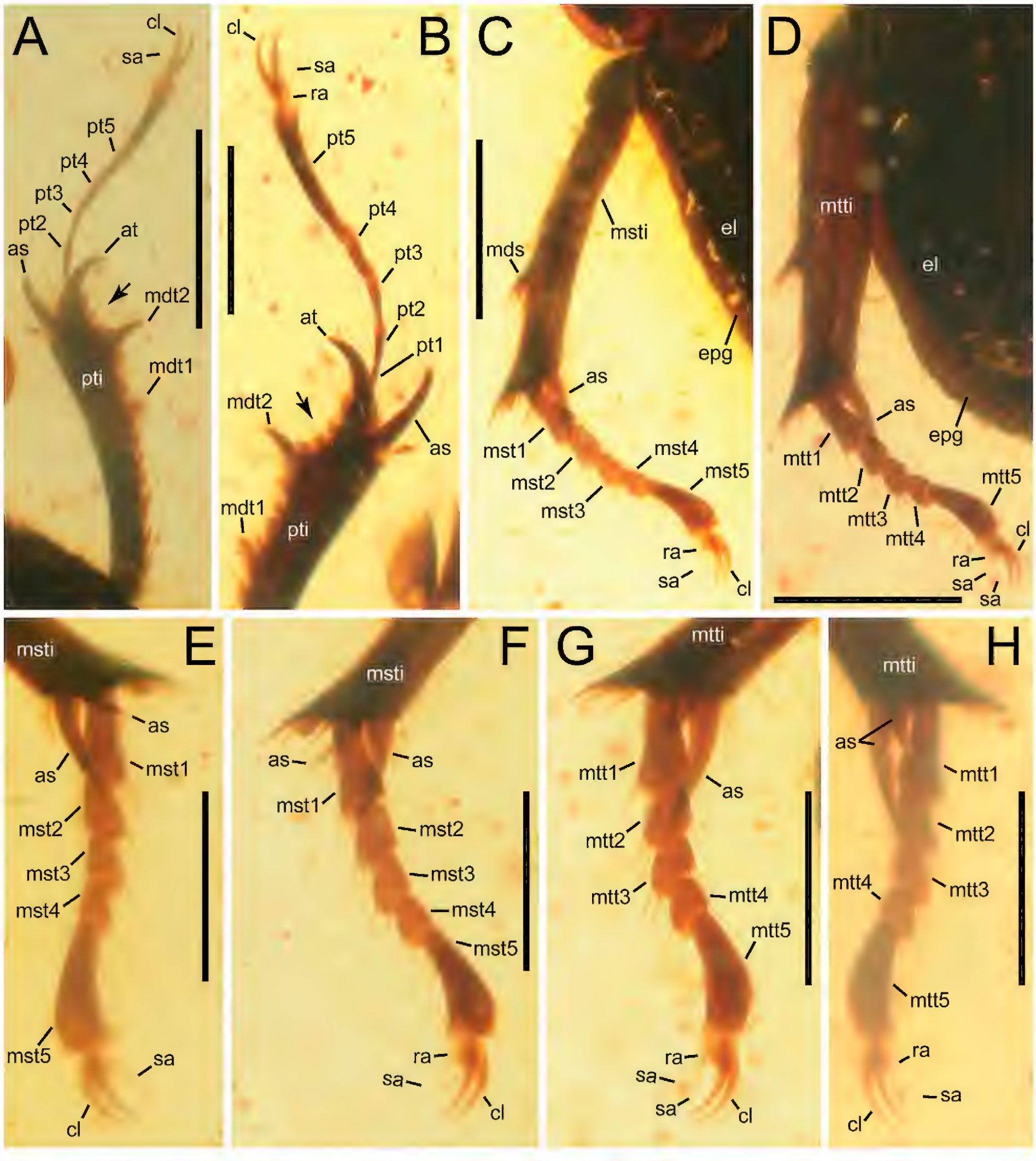

Figure 9. Details of *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206. **A.** Right protibia and protarsus with arrow showing row of small teeth between large spines along outer edge of protibia, dorsal view; **B.** Right protibia with arrow showing row of small teeth between large spines along outer edge of protibia, ventral view; **C.** Left mesotibia and mesotarsus, dorsolateral view; **D.** Left metatibia and metatarsus, dorsolateral view; **E.** Left mesotarsus, ventrolateral view; **F.** Left mesotarsus, dorsolateral view; **G.** Left metatarsus, dorsolateral view; **H.** Left metatarsus, ventrolateral view. Abbreviations: as, apical spur; at, apical tooth of protibia; cl, claw; el, elytron epg, epipleural gutter along outer margin of elytron; mds, mid-dorsal spines of meso- and metatibia; mdt1–2, mid-dorsal teeth 1–2 of protibia; mst1–5, mesotarsomeres 1–5; msti, mesotibia; mtt1–5, metatarsomeres 1–5; mtti, metatibia; pt1–5, protarsomeres 1–5; pti, protibia; ra, rod of arolium; sa, setae on rod of arolium. Scale bars: 0.3 mm (**A**, **C**, **D**); 0.2 mm (**B**, **E**–**H**).

Ceratognathini gen. et sp. indet. 1

Figs 1D, 11, 12.

Material examined. 1 ex. (sex undertemined), a complete adult preserved in a narrowly elongate yellowish amber, approximately 17.1 mm × 6.9 mm × 3.8 mm in size (Fig. 1D); specimen accession number SEHU-0000121207, housed in HUM. The specimen is poorly preserved. The body is noticeably deformed and squashed, although the amber is transparent without pigmentation

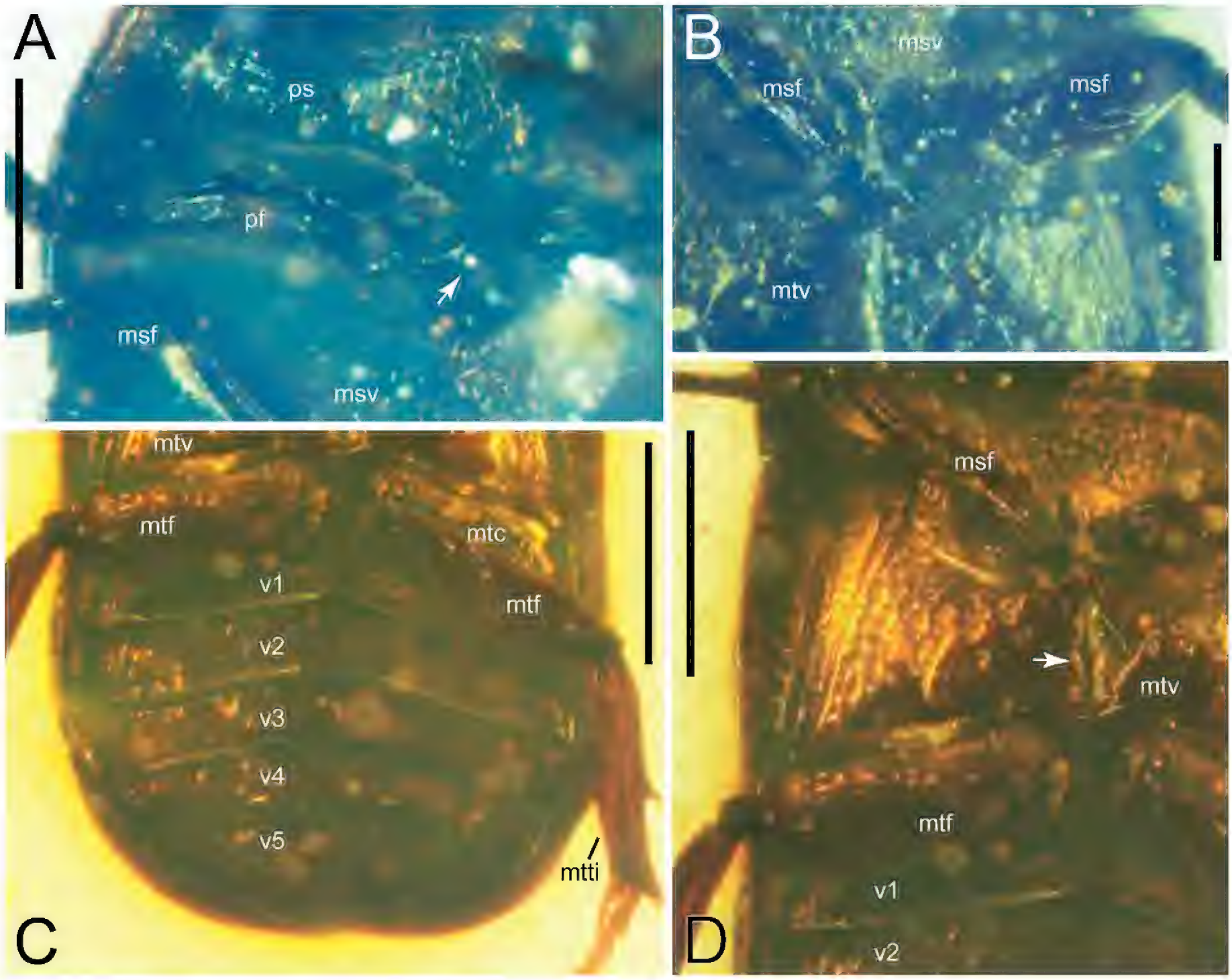

Figure 10. Details of *Cretognathus minutissimus* gen. et sp. nov., holotype, SEHU-0000121206. **A.** Prosternum with arrow showing subcontiguous procoxae, ventral view; **B.** Meso- and metathorax, ventral view; **C.** Abdomen, ventral view; **D.** Meso- and metathorax with arrow showing discrimen (median longitudinal sulcus) on metaventrite, ventral view. Abbreviations: msf, mesofemur; msv, mesoventrite; mtc, metacoxal cavity; mtf, metafemur; mtti, metatibia; mtv, metaventrite; pf, profemur; ps, prosternum; v1–5, ventrites 1–5. Scale bars: 0.3 mm (**A**); 0.2 mm (**B**); 0.5 mm (**C**, **D**).

(Fig. 11). Due to the heavily modified condition of the specimen, it was impossible to make a detailed comparison or accurate measurements of each body part; consequently, only the body length was measured.

Locality and horizon. Hukawng Valley (26°20'N, 96°36'E), Kachin State, northern Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Description. Details of ventral side not well observable. Body (Fig. 11) small, narrowly elongate, subparallel sided, 2.78 mm long (measured from anterior margin of head to apex of elytra). Color uniformly dark brown. Dorsal and ventral surfaces heavily modified, probably due to the fossilization process, without neither setae nor modified scales. Head (Fig. 12A) very small, transverse. Antenna (Fig. 12B–D) seemingly 10-segmented (provisional interpretation shown in Fig. 12B, D) with three-segmented small club (Fig. 3A). Pronotum (Fig. 11A) slightly wider than long, with arcuate lateral margins. Procoxal cavities (Fig. 11B) probably subcontiguous. Elytra (Fig. 11A) complete, narrowly elongate, nearly subparallel-sided. Legs (Figs 11, 12B, E–G) relatively short. Protibia (Figs 11, 12B, E, F) slender, flattened, moderately curved, gradually widened apically, with one large apical spur; external margin armed with three strong teeth in apical half, i.e., apical tooth (*at*) and mid-dorsal teeth 1–2 (*mdt1–2*) (*sensu* Holloway 2007: fig. 1), with about 5 short and subcontiguous tooth-like spines before mid-dorsal tooth 1, 5 between mid-dorsal tooth 1 and mid-dorsal tooth 2, and finally 5 between apical tooth and mid-dorsal tooth 2 (Fig. 12B, arrow). All tarsi (Fig. 12B, E, G) 5-segmented, each slender and rather long. Arolium (Fig. 12E, G, *ra*, *sa*) developed, with short rod, bearing 2 bristles on its apex. Abdomen not well observable. Genitalia not visible.

Systematic placement and comparison. It is challenging to assign the new material to Lucanidae unambiguously based on the available morphology. I could not observe the details of the abdomen to clarify if it has five-free ventrites or clear antennal segmentation. These are important diagnostic features that define the family. However, it is best placed in Lucanidae, more specifically the tribe Ceratognathini, based on the general habitus, 5–5–5 tarsal for-

Figure 11. General habitus of Ceratognathini gen. et sp. indet. 1, SEHU-0000121207. **A.** Dorsal view; **B.** Ventral view. Scale bars: 1.0 mm.

mula, antennae appearing 10-segmented (if correct) with three-segmented apical club, and the structures of legs including protibial outer edges with well-developed arolium between the pretarsal claws (e.g., Ratcliffe 2002; Holloway 2007; Reid 2019). The new specimen lacks modified scales and setae on the dorsal surface, as in *Oncelytris* and the two other Kachin amber ceratognathins recorded here. The extinct taxon is treated provisionally herein as "Ceratognathini gen. et sp. indet. 1" and can be differentiated from *Cretognathus* gen. nov. by having a much smaller head and antennal club, more slender tarsi, and different protibial edges (slightly different arrangement of subcontiguous tooth-like spines and much wider mid-dorsal teeth). Moreover, this new specimen does not seem to be congeneric with "Ceratognathini gen. et sp. indet. 2" by the distinctly smaller head and protibial morphology (shape, size, location, and number of the subequal tooth-like spines). Nevertheless, it is difficult to distinguish it from *Oncelytris*, due to the poor state of preservation of the fossil. In fact, the dorsal and ventral surfaces of "Ceratognathini gen. et sp. indet. 1" are greatly distorted, preventing the accuate observation of the head and elytra whether it possesses tubercles and protuberances on the dorsum or not (cf. Li Y-D et al. 2023). However, it is also noted that the protibiae of "Ceratognathini gen. et sp. indet. 1" is evidently arcuate, whereas those of *Oncelytris* are linear, suggesting that they may belong to different genera.

Ceratognathini gen. et sp. indet. 2

Figs 1E, 13

Material examined. 1 ex. (sex undertemined), a nearly complete adult preserved in a flattened semicircular yellowish amber, approximately 16.7 mm × 6.6 mm × 2.5 mm in size (Fig. 1E); specimen accession number SEHU-0000121208, housed in HUM. Although the specimen appears well-preserved (only slightly modified) with nearly a complete body, the left metatarsomeres beyond the second segment were lost (Fig. 13C). More

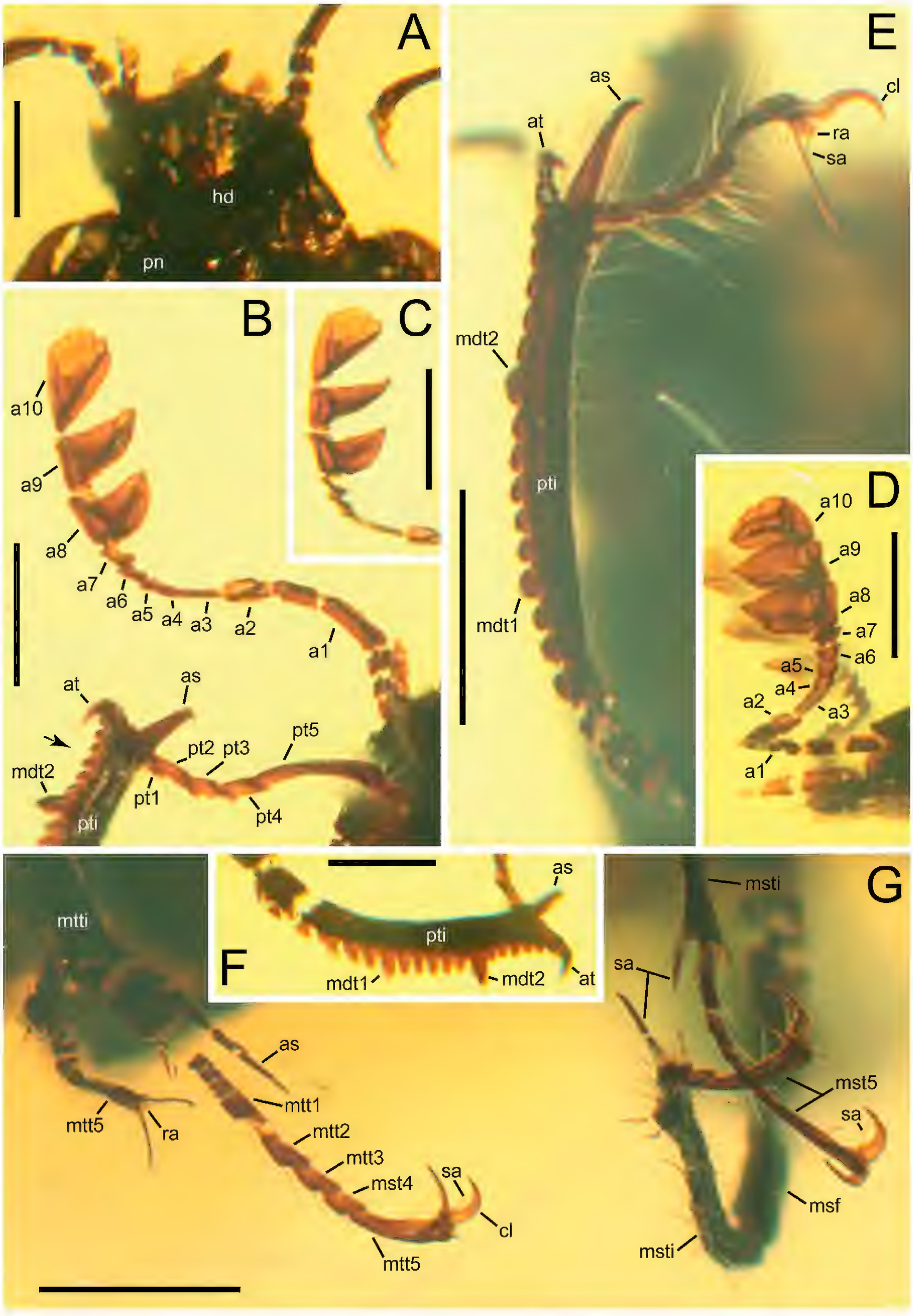

Figure 12. Details of Ceratognathini gen. et sp. indet. 1, SEHU-0000121207. **A.** Head, dorsal view; **B.** Right antenna and apical part of right protibia with protarsus, ventral view; **C.** Right antenna, ventrolateral view; **D.** Left antenna, lateral view; **E.** Right protibia and tarsus, ventrolateral view; **F.** Right protibia, dorsal view; **G.** Mesotarsi and metatarsi, ventrolateral view. Abbreviations: a1–10, antennomeres 1–10 (putative interpretation); as, apical spur; at, apical tooth of protibia; cl, claw; hd, head; mdt1–2, mid-dorsal teeth 1–2 of protibia; mst5, mesotarsomere 5; msti, mesotibia; mtt1–5, metatarsomeres 1–5; mtti, metatibia; pn, pronotum; pt1–5, protarsomeres 1–5; pti, protibia; ra, rod of arolium; sa, setae on rod of arolium. Scale bars: 0.2 mm (**A–F**); 0.3 mm (**G**).

importantly, a thin air layer on the ventral surface of the body makes it difficult to observe the ventral body parts, such as the abdomen and antennae.

Locality and horizon. Hukawng Valley (26°20'N, 96°36'E), Kachin State, northern Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian.

Description. Details of ventral side not uniformly observable. Body (Fig. 13A, B) small, narrowly elongate, subparallel sided, 2.72 mm long (measured from anterior margin of head to apex of elytra). Color uniformly dark brown. Dorsal surface somewhat modified, probably due to the fossilization process, seemingly densely punctured, without neither apparent setae nor modified scales. Head (Fig. 13A–D) small, transverse, 0.60 mm wide across eyes; vertex flattened. Compound eye (Fig. 13A–D, *ey*) large, entire, not divided by ocular canthus. Antennae and mouthparts not visible. Pronotum (Fig. 13A, D) moderately transverse oval, with arcuate and very weakly crenulate lateral margins, 0.92 mm wide and 0.70 mm long (along midline). Elytra (Fig. 13A, C, E) complete, narrowly elongate, nearly subparallel-sided, with left elytron 1.87 mm long (measured from pronotal posterior end to apex of elytron) and 0.45 mm wide; outer margins, particularly those of posterolateral ones, narrowly explanate. Legs (Fig. 13A–C, F, G) relatively short, slender. Protibia (Fig. 13A, B, F) slender, flattened, only weakly curved, gradually slightly widened towards apex, 0.60 mm (left) in length, with one large apical spur (see Fig. 13F, *as*); external margin armed with three strong teeth in apical half, i.e., apical tooth (*at*) and mid-dorsal teeth 1–2

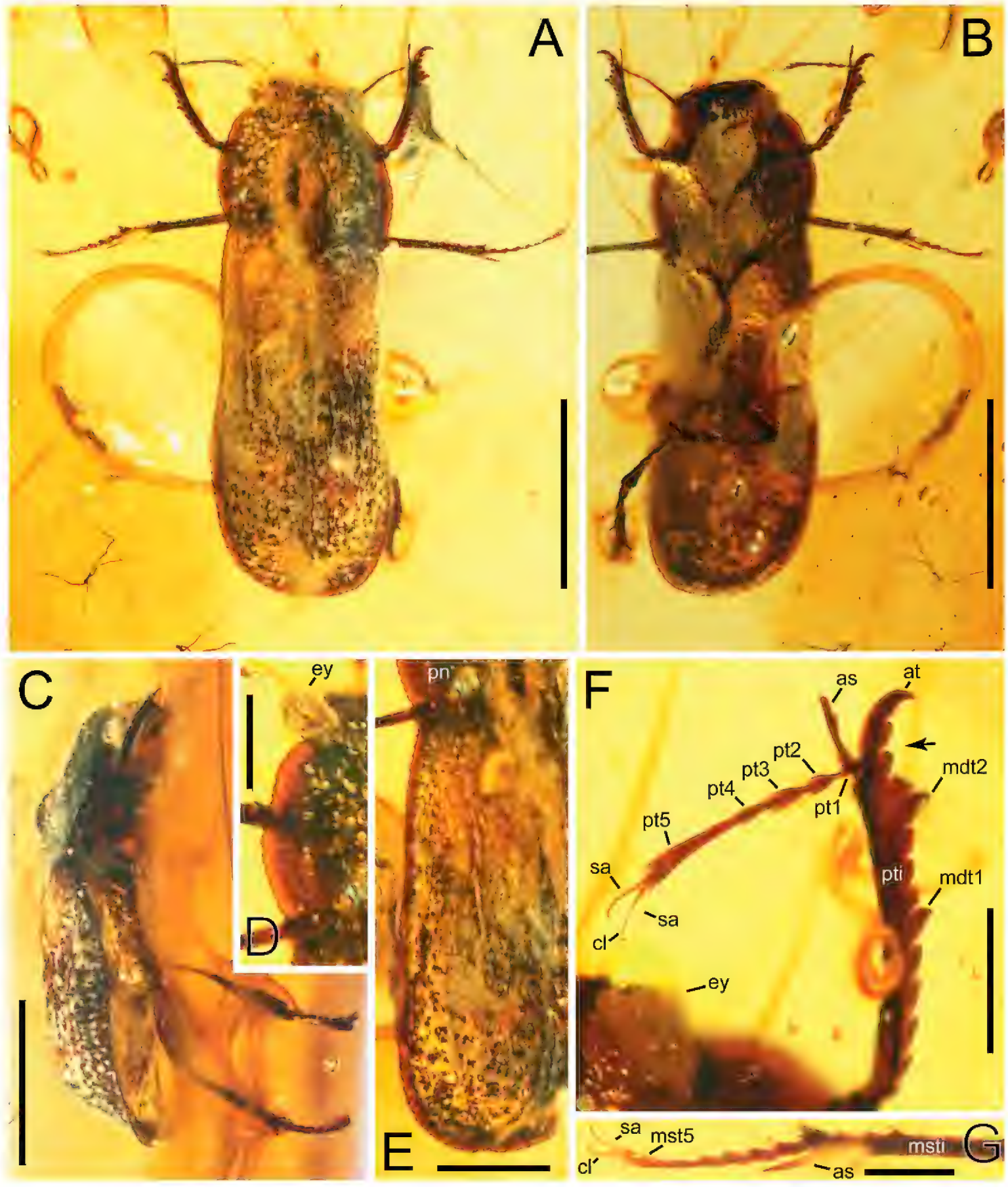

Figure 13. Details of Ceratognathini gen. et sp. indet. 2, SEHU-0000121208. **A.** General habitus, dorsal view; **B.** General habitus, ventral view; **C.** General habitus, lateral view; **D.** Head and pronotum, dorsal view; **E.** Left elytron, dorsolateral view; **F.** Left protibia and protarsus, ventral view; **G.** Left mesotibia and mesotarsus, dorsal view. Abbreviations: as, apical spur; at, apical tooth of protibia; cl, claw; ey, compound eye; mdt1–2, mid-dorsal teeth 1–2 of protibia; mst5, mesotarsomere 5; msti, mesotibia; pn, pronotum; pt1–5, protarsomeres 1–5; pti, protibia; sa, setae on rod of arolium. Scale bars: 1.0 mm (**A–C**); 0.3 mm (**D**); 0.5 mm (**E**); 0.2 mm (**F**, **G**).

(*mdt1–2*) (*sensu* Holloway 2007: fig. 1), with 5 short and subcontiguous tooth-like spines before mid-dorsal tooth 1, 3 between mid-dorsal tooth 1 and mid-dorsal tooth 2, and finally 4 between apical tooth and mid-dorsal tooth 2 (Fig. 13F, arrow). All tarsi (Fig. 13A–C, F, G) 5-segmented, each slender and rather long. Arolium (Fig. 13F, G, *ra*, *sa*) developed, with rather long rod, bearing 2 bristles on its apex. Abdomen not well visible. Genitalia not visible.

Systematic placement and comparison. An accurate definitive assessment of the systematic position of this fossil is difficult; there is no clear view of the ventral side due to a thin whitish air layer, which makes several important features unobservable, such as the abdominal segmentation, details of the antennae, and prosternal process (Fig. 13B). Nevertheless, its putative placement in the lucanid tribe Ceratognathini is supported by the protibial structures, namely the protibial edges have a peculiar arrangement of spine-like teeth (Fig. 13F). Overall, the other features, including the general habitus, head, pronotum, and 5–5–5 tarsal formula, generally agree well with the ceratognathins, particularly the extinct ones described above. Unlike *Oncelytris*, there is no distinct tubercles found on the elytra (see Li Y-D et al. 2023). Based on the structures of the protibial edges, this specimen cannot be assigned to *Cretognathus* gen. nov., "Ceratognathini gen. et sp. indet. 1," or any extant ceratognathin genus. However, this taxonomic consideration as a lucanid is provisional; further visualization and verification is needed for a definitive assignment.

Discussion

Paleodiversity of Lucanidae in Kachin amber

This study added four new lucanid specimens of different taxa to the paleofauna in mid-Cretaceous Burmese (Kachin) amber, doubling the number of known species. While these results clarify the stag beetle fauna of Kachin amber, the identification and systematic placement of one of the two taxa (viz. Ceratognathini gen. et sp. indet. 1, Ceratognathini gen. et sp. indet. 2) in both Ceratognathini and Lucanidae is provisional due to the paucity of morphological information (e.g., the number of abdominal ventrites, and details of the antennae). This is true for paleontological studies of stag beetle fossils in general, as important morphological traits cannot always be identified in many cases or are lacking, which makes it difficult to distinguish them from other beetle families, particularly the superfamily Scarabaeoidea (e.g., Trogidae and Ochodaeidae).

Almost all stag beetle fossils found in Kachin amber are thought to belong or be closely related to the primitive subfamily Aesalinae (or Nicaginae in Li Y-D et al. 2023, *sensu* Howden & Lawrence, 1974) (Cai et al. 2017; Qiu et al. 2017; this study), with the only exception being *Anisoodontus*, which belongs to the derived subfamily Lucaninae (Wu et al. 2022). Within Aesalinae, four species are included in the southern hemisphere tribe Ceratognathini (i.e., †*Oncelytris esquamatus* Li & Cai, 2023; *Cretognathus minutissimus* gen. et sp. nov.; Ceratognathini gen. et sp. indet. 1; and Ceratognathini gen. et sp. indet. 2), while the remaining two belong to the northern hemisphere tribe Nicagini (i.e., *Protonicagus tani* and *P. mandibularis* sp. nov.). Such placements do not contradict the DNA-based divergence time estimate of Kim and Farrell (2015). Consequently, this supports the antiquity of tribes Ceratognathini and Nicagini, as already indicated in Cai et al. (2017) and Li Y-D et al. (2023). Although neither of these tribes are particularly speciose, the discovery of these new fossils further suggests that the paleodiversity of Lucanidae in Kachin amber was rich. This is interesting because the ancient forest that produced Myanmar amber was located at or near the seashore and is thought to have been tropical (Grimaldi et al. 2002; Yu et al. 2019; Burgener et al. 2023), which seems to have of different climate preference of Nicagini. This is because the extant nicagins are known to inhabit sandy areas near large bodies of freshwater such as rivers, lakes, and rarely near small sandy streams, in warm temperate climates (Tabana and Okuda 1992; Paulsen and Smith 2005; Tanahashi 2014). In contrast, Ceratognathini is generally seen in forests of warm temperate regions sometimes with dry periods in New Zealan and South America, as well as the tropics in Australia (Hangay and de Keyzer 2017; Bartolozzi et al. 2017; Tello 2020). Therefore, it is important to remember that environmental preferences may differ between now and the time when Kachin amber was formed. Further research will likely discover many new taxa in the same amber. The present study provides further evidence for the ancient origins of Ceratognathini and Nicagini and their taxonomic diversity.

Morphological implications

The new material reported here retained many plesiomorphic morphological features of stag beetles, such as the undivided eyes, non-geniculate antennae, and inconspicuous mandibles (e.g., Kim and Farrell 2015). These characteristics are generally consistent with those of reported lucanid fossils from Kachin amber. Interestingly, the specimens putatively assigned as Ceratognathini in this study lack well-developed and deformed scales on the body surface (cf. Fig. 15, *scl*; see also Holloway 1997), which could also be considered a primitive state. Even the genus *Anisoodontus*, which is placed in the derived subfamily Lucaninae, lacks developed mandibles, and more importantly, its eyes are not divided (Wu et al. 2022). There are no known fossils from Kachin amber with distinct male mandibles that can be clearly judged as sexual dimorphism, which makes it difficult to explore the evolution of the mandibles in males using this amber. There are older fossil examples with markedly developed male mandibles from the Lower Cretaceous (e.g., Nikolajev and Ren 2015), but they do not preserve some of the morphologies that are important for defining Lucanidae (e.g., the presence of developed arolium) or are difficult to interpret morphologically, so further examination of these fossils is preferable. It is also desirable to obtain specimens that can be identified as male or female, using

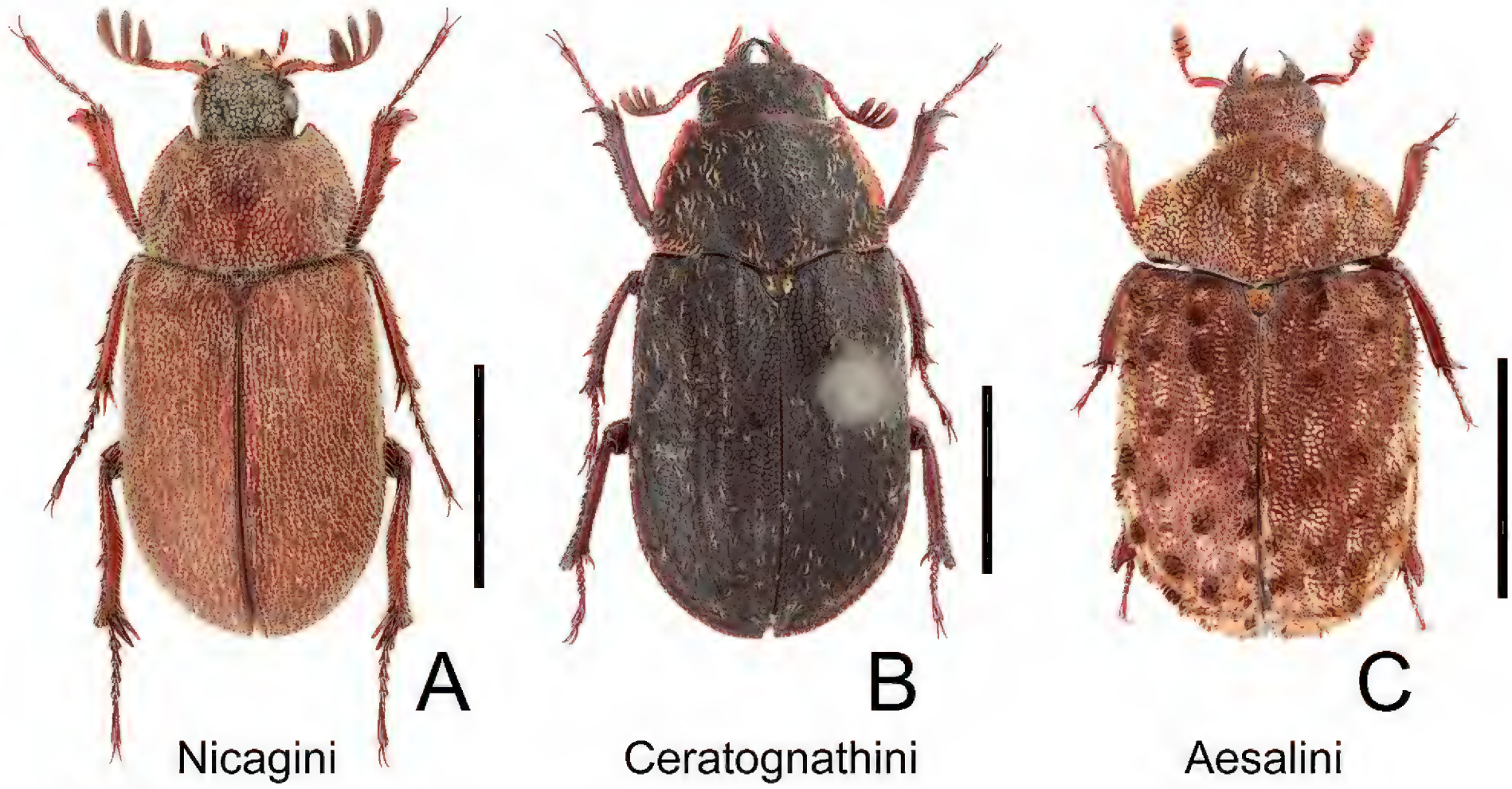

Figure 14. General habitus of extant species of Aesalinae. **A, D.** *Nicagus japonicus* Nagel (tribe Nicagini), male, showing dorsal (**A**) or ventral (**D**) views based on two specimens; **B, E.** *Ceratognathus* cf. *niger* Westwood (tribe Ceratognathini), female, showing dorsal (**B**) or ventral (**E**) views based on same specimen; **C, F.** *Aesalus asiaticus asiaticus* Lewis (tribe Aesalini), female, showing dorsal (**C**) or ventral (**F**) views based on two specimens. Scale bars: 3.0 mm.

additional specimens with exposed genitalia, or based on further examinations by X-ray micro-computed tomography and phase-contrast X-ray synchrotron microtomography for three-dimensional (3D) reconstructions.

Miniaturization trend

Stag beetles are extremely varied in body size, with males reaching 120 mm including the elongated mandibles, as seen in *Prosopocoilus giraffa keisukei* Mizunuma & Nagai (Fujita 2010). By contrast, some Aesalini (Aesalinae) are much smaller, with the smallest one being only 3 mm in length (Fujita 2010). All four specimens reported here are extremely small, measuring a maximum of 3.6 mm, with three clearly less than 3 mm, unless incorrect identification or deformation affected the two provisionally identified specimens. However, *Cretognathus minutissimus* gen. et sp. nov. has no noticeable deformities and its head projects forward in a natural way, but it is only 2.83 mm long with mandibles. No extinct lucanids this small have ever been reported (e.g., Nikolajev et al. 2011); therefore,

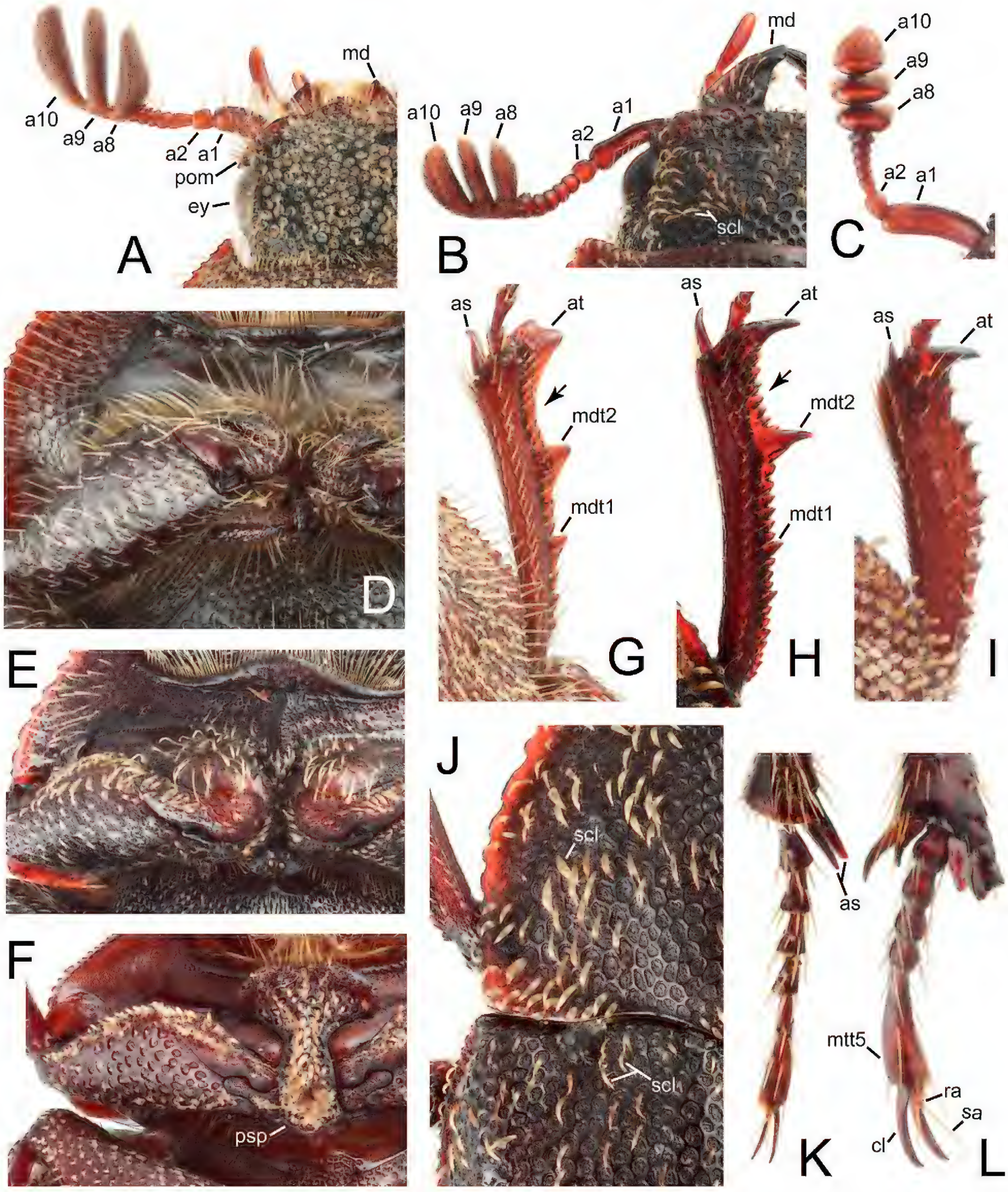

Figure 15. Details of extant species of Aesalinae. **A, D, G, K.** *Nicagus japonicus* (tribe Nicagini), male, showing head with left antenna in dorsal view (**A**), prosternal process (intercoxal process of procoxae) with subcontiguous procoxae in ventral view (**D**), right protibia in dorsal view (**G**), or right metatarsus in ventral view (**K**) based on two specimens; **B, E, H, J, L.** *Ceratognathus* cf. *niger* (tribe Ceratognathini), female, showing head with left antenna in dorsal view (**B**), prosternal process (intercoxal process of procoxae) with subcontiguous procoxae in ventral view (**E**), right protibia in dorsal view (**H**), pronotum and left elytron with scales (**J**), or left metatarsus in ventral view (**L**) based on same specimen; **C, F, I.** *Aesalus asiaticus asiaticus* (tribe Aesalini), female, showing left antenna in dorsal view (**C**), prosternal process (intercoxal process of procoxae) with separated procoxae in ventral view (**F**), or right protibia in dorsal view (**I**) based on two specimens. Arrows show either smooth (**G**) or serrate outer edge **(H)** between mid-dorsal tooth 1 and mid-dorsal tooth 2 of each protibia. Abbreviations: a1, a2, a8–10, antennomeres 1, 2, 8–10; as, apical spur; at, apical tooth of protibia; cl, claw; ey, compound eye; md, mandible; mdt1–2, mid-dorsal teeth 1–2 of protibia; mtt5, metatarsomere 5; psp, prosternal process between procoxae; ra, rod of arolium; scl, scales on head, pronotum, and elytra; sa, setae on rod of arolium.

three of the fossils reported here represent the smallest stag beetles among all known extant and extinct species.

Several species across insect orders (i.e., Coleoptera, Hymenoptera, Thysanoptera, and Hemiptera) found in Kachin amber are clearly smaller than their extant counterparts (e.g., Li L et al. 2017; Yamamoto and Takahashi 2018, 2019; Żyła et al. 2019; Li Y-D et al. 2020; Souma et al. 2021; Tokareva et al. 2023), particularly beetles. Although, not all Coleoptera described from Kachin amber are distinctly smaller than extant representatives (Jenkins Shaw and Żyła 2020; Tokareva et al. 2023). It is difficult to ascertain the exact factors contributing to this miniaturization phenomenon, but it might be attributable to random variation during the evolution of each group over time, or perhaps to the temperature and oxygen levels at that time (Liu et al. 2021), rather than just being a taphonomic artefact (see also Song et al. 2022).

Paleobiogeographic implications

This paper reports three lucanid taxa putatively related to Gondwana: *Cretognathus minutissimus* gen. et sp. nov.; Ceratognathini gen. et sp. indet. 1; and Ceratognathini gen. et sp. indet. 2. All three were assigned to the extant austral tribe Ceratognathini, currently known from Australia and New Zealand (Holloway 2007; Bartolozzi et al. 2017; Hangay and de Keyzer 2017; Reid 2019), although two assignments are provisional (see above). The newly discovered *Oncelytris* from Kachin amber was also placed in this tribe (Li Y-D et al. 2023).

Interestingly, recent research on Kachin amber has led to the discovery of animals and plants that are thought to be Gondwanan elements (summarized in Poinar 2019), including beetles. For example, fossils of the monotomid tribe Lenacini, endemic to New Zealand, have been found in Kachin amber (Liu et al. 2020), including the extant genus *Lenax* Sharp and an extinct genus with two species unique to Kachin amber. In addition, the ommatid genus *Omma* Newman, erotyloid family Boganiidae, and cucujoid family Cyclaxyridae, which have been found in Kachin amber, are all endemic to either Australia or New Zealand (e.g., Cai et al. 2018; Gimmel et al. 2019; Li Y-D et al. 2021). Nevertheless, the latter three examples refute a strict historical Gondwanan distribution, because fossils have also been found in the Northern Hemisphere, highlighting relictualism in Australasia (e.g., Cai et al. 2018; Gimmel et al. 2019; Li Y-D et al. 2021). Moreover, beetle taxa associated with the Northern Hemisphere have also been reported from Kachin amber (e.g., Cai and Huang 2018; Li Y-D et al. 2019; Yamamoto and Newton 2023), including *Protonicagus*, which was treated in this study. More studies are needed to clarify the detailed distributions of beetles and whether they are the truly of Gondwanan origins or merely relict distributions in Pangaea.

The Burma Terrane, also called the West Burma Block, which produced Burmese amber, formed an island located near the Australian block in East Gondwana during the Early Jurassic (Heine et al. 2004; Heine and Müller 2005; Seton et al. 2012; Westerweel et al. 2019). Subsequently, it was uplifted northward by tectonic activity, and geographically isolated as an island in the Tethys Ocean between Asia and the Indian block during the mid-Cretaceous for more than 20 Ma (see details in Jouault et al. 2021 and references therein). Such a peculiar palaeogeographic history is thought to have contributed to the uniqueness of the Burmese amber biota (Westerweel et al. 2019). The discovery of four lucanid fossils presented here expands our understanding of the evolutionary history and paleobiogeography of stag beetles.

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